

# THE EVOLUTION OF GÖSSYPIUM



EMPIRE COTTON GROWING CORPORATION

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# THE EVOLUTION OF GOSSYPIUM

AND THE DIFFERENTIATION OF  
THE CULTIVATED COTTONS

by

J. B. HUTCHINSON, R. A. SILOW and S. G. STEPHENS

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## PREFACE

THE closing of the Cotton Research Station in Trinidad, and the decision to pursue research on the genetics of cotton in closer contact with the commercial crop in Africa, marks a stage in the development of the research policy of the Empire Cotton Growing Corporation at which recent additions to knowledge of the world's cottons may suitably be reviewed.

When the Trinidad Station was started in 1926, cotton was botanically one of the less well-known crop plants, and it was recognized that comprehensive studies of the botany and genetics of the genus *Gossypium* were required if an adequate foundation of knowledge was to be provided for the cotton breeder. The programme initiated in the Genetics Department to meet these needs developed along three main lines. Cottons and cotton relatives were collected from all parts of the world and current classifications of the genus were reviewed in the light of experience with living material. A genetics programme was undertaken that was designed to elucidate the differences in gene content responsible for racial, varietal and specific differences among the cultivated cottons. Out of these two arose the need for an inquiry into the wider relationships of the wild and cultivated species, and cytological studies were added.

The results of these investigations have been published from time to time, and are included in the Memoirs of the Cotton Research Station, Series A, Genetics. The task here attempted is that of reviewing the genus as a whole, and of presenting an account of its evolution and present status which is sufficiently broadly based on experimental evidence to be generally acceptable to cotton workers, and which fulfils the primary aim of the Genetics Department of providing an adequate foundation of knowledge for the proper planning of cotton breeding work.

The extent to which we have made use of published work is indicated by the bibliography, but there are contributions to the progress of cotton research that are not adequately acknow-

ledged by reference to the literature. The adoption by the Empire Cotton Growing Corporation of the far-sighted policy which made possible the pursuit of fundamental botanical and genetic studies on cotton at the Cotton Research Station was largely due to the influence of the late Sir James Currie, K.C.M.G., K.B.E., and the late Sir John Farmer, F.R.S. The share of two former members of the staff of the Station in implementing that policy requires acknowledgment. The solution of the major problems involved in the genetics of the cultivated cottons followed Dr. S. C. Harland's successful attack on the modifier problem, and this led directly to his concept of the nature of the species distinction, on which the present system of classification depends. Likewise, the elucidation of wider relationships in the genus followed from Dr. A. Skovsted's extensive hybridization experiments, which radically altered former ideas on crossing behaviour, and his cytological studies, which largely mapped out the cytological situation.

Collaboration between cotton workers in different countries has always been close, and members of the Cotton Research Station staff are indebted to men in many parts of the world for assistance with both material and information. No acknowledgment would be complete without reference to the contributions made by Dr. T. H. Kearney, of the United States Department of Agriculture, to the Station collection of wild and cultivated species, and by Dr. J. M. Webber, also of the United States Department of Agriculture, to the elucidation of the cytology of *Gossypium*.

The cytological work of Dr. J. O. Beasley has been of great importance in the development of the argument put forward in Part II, and we wish to record our sense of loss at the news of his death on active service.

No adequate interpretation of the status of the Indian cottons would have been possible without the extensive knowledge of their history and characteristics put at our disposal by Rao Bahadur V. Ramanatha Ayyar. Much information concerning the cottons of China has been supplied by Mr. Chi-Pao Yu, whose contributions to cotton genetics have been made under the extremely difficult circumstances of the war with Japan.

The classification section owes much to the late Dr. J. Burt Davy, to Mr. J. E. Dandy, and to Miss D. Hillcoat. The photographs reproduced as Plate III were kindly supplied by Dr. T.

H. Kearney of the United States Department of Agriculture, and by the Keeper of Botany, British Museum (Natural History). For the rest of the Plates and the maps we are indebted to Mr. F. Whitburn.

31 December 1944

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## PART ONE

### THE CLASSIFICATION OF THE GENUS '*Gossypium*'

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#### I. INTRODUCTION

THE taxonomy of cultivated crop plants is beset with difficulties, the nature of which has only become clear as a result of recent studies of their genetics and geographical distribution. Their great variability, often concentrated in a small part of their geographical range, has led taxonomists either to describe a multitude of forms as species, or to postulate primitive, well separated species which have subsequently come together and given rise by hybridization to the welter of forms now observed. The recognition of the true nature of this variability dates from Vavilov's (1935) demonstration that the areas where it is greatest are the areas in which the crop originated, or at least has been established longest. His conclusion that variability is primitive in cultivated plants, and not the consequence of recent hybridization, has been amply supported in cotton by Mauer (1930), Hutchinson and Ghose (1937a, 1937b), and Hutchinson (1938). The concept of the species has consequently been broadened and simplified so that only those groups which differ in genetical architecture, or between which genetic or cytological barriers exist, are regarded as separate species. Since the morphological distinctions associated with real genetic differences can only be determined with certainty by genetic analysis, revision of the taxonomy of cultivated crop plants is only profitable after extensive genetic and cytological studies have been made. Such studies are well advanced in *Gossypium* and it is considered that the time is ripe for the preparation of a classification that will be at once soundly based on genetic and cytological data, and acceptable to systematic botanists as a reasonable and natural account of the plant species related to the commercial cottons.

## II. PREVIOUS LITERATURE

WATT'S (1907) monograph will always remain the starting point for taxonomic studies in *Gossypium*. For detailed records of herbarium material, literature and early classifications his work is invaluable. Papers quoted from Watt (1907) are indicated by the insertion of W after the date, and are not included in the list of references. His records of herbarium material were supplemented by two later papers (Watt, 1926, 1927). Recent literature is discussed by Hutchinson and Ghose (1937b).

Current ideas on the classification of *Gossypium* date from a paper by Zaitzev (1928). They were elaborated from the genetic viewpoint by Harland (1932a, 1939, 1940a) using data from his own investigations. In an attempt to give due weight to morphological considerations Hutchinson and Ghose (1937b) amplified the classification of the cottons of Asia and Africa, combining a study of the cotton specimens in the herbarium of the Royal Botanic Gardens, Calcutta, with their investigations on genetics and crop ecology.

Reference must also be made to Roberty's (1938) recent work, but he has failed to give sufficient weight to genetic evidence, and his arrangement cuts across well established natural groupings in several important respects.

### III. THE RELATIONSHIPS OF THE GENUS

THE classification of certain taxonomic groups in the Malvales has been revised by Edlin (1935). It is not intended here to discuss in detail the generic and family affinities of *Gossypium*, but a summary of his classification and of the relationship of *Gossypium* to the rest of the Hibisceae forms a convenient background for the description of the specific and varietal composition of the genus.

Edlin considers the Scytopetalaceae the most primitive of the Malvales, followed by the Tiliaceae. From the latter, three families diverged, the Sterculiaceae by the development of apocarpy, apetaly, and unisexuality, the Buettneriaceae by the union of stamens, reduction of stamens, or the development of regular staminodes, and the Bombacaceae and Malvaceae by the development of unilocular anthers. He regards the Malvaceae as more advanced than, but in the same sequence as, the Bombacaceae. He separates them on the character of the fruit, limiting the Malvaceae to genera with septicidally dehiscent schizocarps and including all those with loculicidally dehiscent (capsular) or baccate fruits in the Bombacaceae. The whole of the Hibisceae are thereby transferred from the Malvaceae to the Bombacaceae. There are certain advantages in this arrangement. The trees and woody shrubs are all included in the Bombacaceae and the Malvaceae confined to herbaceous or only softly woody plants. From the economic point of view the species producing seed and capsule hairs are all included in one family, as are also most of the important host plants of pests attacking *Gossypium*.

The genera of the Hibisceae fall into a large group with spreading style branches, capitate or dilated stigmas, and reniform seeds, and a small group, including *Gossypium*, with styles usually clavate and furrowed, or divided into stigmatic branches that are usually erect, rarely divided at the tip or capitate, and with the seeds rounded or turbinate, sometimes compressed, but not reniform. The characters of importance in the separation of

the genera of the latter group are: (a) the type of inflorescence; (b) the number, size and persistence of the bracteoles; (c) the form of the calyx; (d) whether the style is clavate or branched; (e) the distribution of the black oil glands; (f) the character of the fruit; and (g) chromosome number. The range of variation in these characters, so far as it is known, is tabulated on page 5.

*Cienfugosia* is predominantly African and American in distribution. There has been considerable confusion between it and *Gossypium*, and the allocation of some African species to *Gossypium* is proposed below. Lewton (1915) states that the true *Cienfugosias* have the oil glands arranged in rows on the sepals, whereas in *Gossypium* they are distributed at random, and on this character it should not be difficult to assign doubtful species. On this point Dr. Silow states that, 'On the whole, oil glands in rows on the sepals appears to be a valid criterion of *Cienfugosia* as restricted by Lewton by his removal of species referred to *Notoxylinon* and *Alyogyne* (see below), though the glands may be extremely few as in the case of *A. hakaefolia* and therefore not easily classifiable, or their departure from linear arrangement only slight, as in some forms of *N. australe*, a condition approached by *C. argentina* Garcke; whilst in some cases it is very difficult to discern the oil glands at all beneath a thick covering of hairs as in some forms of *C. phlomidifolia* Garcke f. Schum., or in *Fugosia gerrardi* Harv.'

Chevalier (1933) and Skovsted (1935c) independently transferred *Gossypium anomalum* from *Cienfugosia*, and the distribution of the oil glands and the form of the calyx are in accord with the genetic and cytological evidence in this species. Skovsted (1937) also suggested that *Cienfugosia triphylla* Harv. should properly be included in *Gossypium*. From an examination of specimens in the U.S. National Herbarium and in the Arnold Arboretum Herbarium (K. Dinter No. 5,502; Otavi, South-west Africa), Silow concluded that 'this species should be transferred to *Gossypium*. In form of calyx teeth, distribution of oil glands on calyx, size of linear acute bracteoles (which are here entire), colour of corolla and size of petal spot (cf. Silow, 1941), size, shape and nature of capsule, size and shape of seed, with a single coat of fine brown hairs, non-self-expansive, up to 10 mm. long, and short downy tomentum on leaves, it bears very strong similarity in general appearance to *G. anomalum*.' The Somaliland species described as *Cienfugosia somalensis*,



## DIAGNOSTIC FEATURES OF 'GOSSYPIUM' AND RELATED GENERA

<i>Inflorescence</i>	<i>Bracteoles</i>	<i>Calyx</i>	<i>Style</i>	<i>Oil Glands</i>	<i>Fruit</i>	<i>Chromosome number (n)</i>
<i>Cienfuegosia</i> (including <i>Redoutia</i> ) Flrs. axillary, or on jointed peduncles, rarely on sympodial branches	0-15, linear, often minute.	Deeply 5-parted.	Clavate, capitate, or with free style branches.	Arranged in lines on the sepals, irregularly elsewhere.	Carpels thin, dry and brittle.	10 and 11 (many unknown)
<i>Gossypium</i> Sympodium, jointed peduncle or spur	3, foliar, linear, or minute. Persistent or caducous.	Truncate, 5-undulate or 5-pointed.	Clavate. Rarely slightly divided at tip.	Irregularly arranged throughout the plant.	Fruit glabrous. Carpels thin, dry and brittle.	13 and 26.
<i>Gossypoides</i> Sympodium	3, foliar, persistent.	Truncate, 5-undulate.	Stigmas free, equal to carpels in number.	Irregularly arranged throughout the plant.	Carpels thin, dry and brittle.	12.
<i>Kokia</i> Jointed peduncle with caducous bract at joint	3, foliar, persistent.	Truncate, 5-undulate.	Clavate.	Irregularly arranged throughout the plant.	Woody.	12.
<i>Thespesia</i> Flrs. axillary, or on jointed peduncles or sympodial fruiting branches	(including <i>Montezuma</i> , <i>Maga</i> , <i>Armouria</i> , <i>Shantzia</i> , and <i>Azanza</i> ) 3-15, small, caducous.	Truncate, or drawn out into long teeth, persistent or circumsessile.	Clavate.	Inconspicuous.	Fruit often hairy, at least when young. Carpels woody or leathery, sometimes thin and brittle.	13 (many unknown)
<i>Notoxylinon</i> (see Lewton 1915) Flrs. axillary, or on jointed peduncles or sympodial fruiting branches	3, linear. Persistent or caducous	5-toothed, or deeply 5-parted.	Clavate.	Irregularly arranged. Absent from cotyledons.	Woody.	Not known.
<i>Albugyne</i> Flrs. on thickened peduncles	(see Lewton 1915) Shallow 5-7-toothed cup.	Deeply 5-parted. Sepals lanceolate.	Clavate.	Irregularly arranged. Not in cotyledons.	Not stated.	Not known.

*C. ellenbeckii*, *C. bricchettii* and the Arabian species *Fugosia areysiana* are also transferred to *Gossypium* below.

*Kokia* was separated from *Gossypium* by Lewton (1912b) and the separation is abundantly justified. The habit of the plants, the type of inflorescence, the fruit and the chromosome number are all characteristic, and distinct from *Gossypium*. The genus is endemic in Hawaii.

*Gossypioides* has been proposed by Skovsted (1935c) as a separate genus for the East African shrub formerly named *Gossypium kirkii*, the exclusion of which from *Gossypium* was first proposed by Harland (1932a). The endemic Madagascar species *Gossypioides brevilanatum* is evidently related to the East African one, though widely different in several important characters (Hutchinson, 1943a). Both species differ from *Gossypium* in their ribbed or winged stems, free stigma lobes, and chromosome number ( $n = 12$ ). The group is distinct from cotton in leaf form and general appearance, and all attempts at hybridization or grafting with *Gossypium* species have failed. Their separation as the genus *Gossypioides* is therefore accepted. A detailed description is given by Hutchinson (in press).

The arrangement of the *Thespesia* group of genera requires further study. *Thespesia populnea*, and the species included in *Montezuma* (Maga) and *Armouria* have axillary flowers with three bracteoles, and leathery or woody fruits. *Thespesia populnea* is circumtropical, but the remaining species are endemic in the Greater Antilles. The chromosome number is  $n = 13$  in *T. populnea*. *T. garckeana* is an African species and differs from *T. populnea* in having the flowers borne on jointed peduncles and having 9—15 bracteoles. Its chromosome number is  $n = 13$ . These species are all easily distinguished from *Gossypium* by their woody or leathery fruits. *T. lampas* is an Asiatic species. It differs from the rest of *Thespesia* in the inflorescence, which is sympodial, the bracteoles, which are 3—6 in number, the carpels, which are thin and brittle, or only slightly woody, when ripe, and the seeds, which are turbinate and not compressed. The chromosome number is  $n = 13$ . It differs from *Gossypium* in the number of the bracteoles.

All species of the *Thespesia* group that have been examined have the same basic chromosome number as *Gossypium*, and their affinity with *Gossypium* is shown by the graft compatibility of *T. populnea* and *T. lampas* with *Gossypium sturtii*, and by the

development of capsules (containing empty seeds) when *Gossypium anomalum* was pollinated by *T. lampas* (Stephens, unpublished data).

*Notoxylinon* and *Alyogyne* were established by Lewton (1915) to include endemic Australian species that had been placed by various authors in *Gossypium*, *Cienfugosia* (*Fugosia*) and *Hibiscus*. From *Hibiscus* they are distinguished by their clavate styles, and from *Cienfugosia* by the irregular distribution of the black oil glands on the sepals. From *Gossypium*, Lewton (1915) distinguished them by the absence of black oil glands from the cotyledons. He stated that he did not consider that *Gossypium* was represented in Australia, except by cultivated plants. Black oil glands are present in the cotyledons of the Australian *G. sturtii*, however, and recent work (Skovsted 1935b, Webber 1939) has shown that this species is undoubtedly related cytologically to the true cottons. Examination of Gardner's recent collections of *G. robinsonii* (Lewton's *Notoxylinon robinsoni*) has convinced the author that it is not generically distinct from *G. sturtii*. I am indebted to Dr. R. A. Silow for the following note on *Notoxylinon* material in several American herbaria: 'Lewton's eight species of *Notoxylinon* were separated by him into two series, the first with calyx truncate, the second with calyx 5-parted or deeply lobed. Such a description as 'truncate calyx' suggested that the species so described might not be clearly delimited from *Gossypium*. Examination of photographic material of the first two of the three species which Lewton assigned to this section of *Notoxylinon* showed that their calyx teeth are actually much longer than is usual in *Gossypium*. On the other hand *robinsonii*, which Lewton included in his section of the genus with calyx 5-parted or deeply lobed, has a calyx which is merely undulate, as is typical of *Gossypium*. Eliminating this species from *Notoxylinon*, there should in general be no difficulty in separating this genus from *Gossypium* on the basis of well-marked calyx teeth. Furthermore, with additional information, it will probably transpire that both seed shape and the nature of the hairy covering on the testa are constant diagnostic features. The seeds of the one *Notoxylinon* seen, *australe*, agree with those of the *Cienfugosias* seen in being relatively small, narrow, elongated and pointed, with a covering of short, straight, non-intertangled hairs, almost bristly in comparison with those of *Gossypium*.'

The two species of *Alyogyne* are succulents, and are easily distinguished from the other genera in the group.

No comparisons of the variability of these genera can be made while knowledge of the limits of some of them—notably *Notoxylon*, *Cienfugosia* and *Thespesia*—is incomplete, but it is worthy of note that in several important characters there is to be found in *Gossypium* practically the whole range of variation in the group. The inflorescence varies from a fully developed sympodium in the true cottons to a jointed peduncle (such as occurs in *Thespesia*, *Cienfugosia* and *Kokia*) in the **Section Erioxyla**. The bracteoles may be large, foliar and persistent, or small and linear, minute, or in some cases caducous. The calyx may be shortly truncate, undulate, or 5-pointed. The leaves may be broad entire, shallowly or deeply lobed, or even narrowly lanceolate entire. Many of the species differing most from typical *Gossypium* were originally described as monotypic genera (*Ingenhouzia*, *Thurberia*, *Selera*, *Erioxylum*, and *Sturtia*) and their inclusion in *Gossypium* has been established by genetic and cytological research.

#### IV. THE DELIMITATION OF THE SPÉCIES

THE cytological situation in *Gossypium* has been worked out by Skovsted (1933-7) and Webber (1939), and their findings have recently been confirmed and amplified by Beasley's (1942) and Stephens's (1942) studies of artificially induced polyploids. The basic chromosome number in the genus is  $n=13$ , and all species have either  $n=13$  or  $n=26$ . The species with  $n=13$  chromosomes fall into five major groups between which, with one exception, chromosome homology is low. These are: the wild Australian species; the wild American species; the wild African and Arabian species; the wild species of Northern India and Arabia, and Somaliland; and the cultivated species of the Old World. The cottons with  $n=26$  chromosomes carry a complement which consists of a set of 13 homologous with the genom of the cultivated Old World species and a set of 13 homologous with that of the wild American species. Crosses between species belonging to different main groups are usually difficult to make, and in some cases impossible, and when successful give highly sterile  $F_1$  hybrids.

It will be shown in Part II that these six groups represent major lines of evolutionary differentiation. For taxonomic purposes it is also convenient to recognize among the American wild species a subsidiary morphological grouping, which generally represents a lower order of differentiation, but may group together species that have become morphologically similar by convergence. The American group is subdivided into three, making in all eight species groups or **Sections**.

**Section I Sturtiana** includes the wild Australian species.

The New World wild species contribute **Sections** II, III, and IV. Between the species of this group some crosses fail, and some result in partially sterile  $F_1$ s. Where later generations have been raised they usually contain a large proportion of weak or unthrifty plants, and such genetic information as is available indicates wide divergence in gene constitution. Cytological studies show, however, that chromosome homology is high. While cytogenetic data lead to no very satisfactory arrangement

of the species, on morphological characters they fall into three well defined, natural **Sections**. These may be distinguished on the nature of the leaf, the plant hairiness, the bracteoles, and the fruiting branches. In **Section II Erioxyla** the leaves are entire or only very shallowly lobed, the plants glabrous or finely hairy, the bracteoles entire or nearly so, much reduced or caducous at anthesis, and the fruiting branches almost always reduced to jointed peduncles or leafless spurs. In **Section III Klotzschiana** the leaves are entire, the plants tomentose, the bracteoles many-toothed, large and persistent, and the fruiting branches many-jointed, or at least two-jointed in a large proportion of cases (*G. raimondii*). In **Section IV Thurberana** the leaves are deeply lobed, the plants glabrous or finely hairy, the bracteoles entire or nearly so, sometimes reduced, and the fruiting branches many-jointed.

**Section V Anomala** includes *G. anomalum*, *G. triphyllum* and *G. areysianum*. Of these, only the first has been grown in culture, and the two latter are included with it on morphological grounds only. **Section VI Stocksiana** includes *G. stocksii* and *G. somalense*. The latter has not yet been studied experimentally, and is included on morphological grounds. In **Section VII Herbacea** are included the species to which the cultivated cottons of the Old World belong. All species in these three **Sections** that have been grown in culture will intercross, but all *G. stocksii* hybrids are completely sterile, and some of them are feeble. Cytogenetically *G. stocksii* appears to be a very isolated species. Crosses between *G. anomalum* and cultivated Old World cottons are very slightly fertile, and chromosome homology between them appears to be high. Within the **Section Herbacea** interfertility and chromosome homology are very high.

The  $n = 26$  chromosome cottons include the cultivated New World species, and the wild *G. tomentosum* from Hawaii. Chromosome homology and fertility between them are high, and they form a natural **Section** (VIII **Hirsuta**).

The species included in the last two **Sections** are the only ones that bear true lint hairs, and it is from them that the cotton of commerce is derived. The seed hairs of the wild species are cylindrical in cross section. Lint hairs, on the other hand, collapse on drying, forming flat, spirally twisted ribbons.

Among the domesticated species, the great variability characteristic of cultivated crop plants led to the separation as

species of a large number of types distinguished on one or a few characters that can now be shown to be genetically simple and unimportant. The first-fruit of genetic studies was the merging of such species in larger units, and the question then arose whether there are any natural species distinctions within the inter-fertile groups or whether the whole range of variation is continuous. The existence of genetic discontinuities within both Old World and New World cultivated cottons was soon demonstrated, and Silow (1944b) has recently followed the sequence of their development from the earliest stages of divergent selection within a single population to the degree of differentiation that results in almost complete sterility. He has shown that the beginnings of differentiation do not depend upon the total amount of variability present, but upon its distribution. When character combinations occur at random there is no possibility of making a rational subdivision in even highly variable species, whereas the orderly assortment of characters in groups, particularly when the groups are geographically isolated, results in the appearance of a natural varietal subclassification.

In isolated populations progressive genetic divergence leads to increasing differentiation of the internal environment, so that a gene which will combine harmoniously with the genotype of one of two separating groups fails to act satisfactorily in the other. In this way races carrying what Harland (1936) called 'co-ordinated modifier complexes' are built up, each one harmoniously integrated to give a balanced genotype, but so different in gene content as to give rise to extensive polygenic segregation in crosses between them. The majority of the products of recombination in such crosses are less well-balanced genotypically than the parent types, and consequently fail to compete against them, while extreme types are weak and partially sterile. Thus a barrier is built up which, while not absolutely precluding the exchange of genes between one group and the other, ensures the elimination of intergrading types by natural selection. Groups between which the existence of such a barrier has been demonstrated are here regarded as specifically distinct.

That the breakdown of genotypic balance in interspecific hybrids in cotton is a factor of real importance in the maintenance of species distinctions is shown by studies of crops in which two species are grown mixed. In parts of the Madras Presidency in South India and in Kathiawar, Western India, it is the cus-

tom to grow mixtures of *G. herbaceum* var. *acerifolium* and *G. arboreum*. First generation hybrids are not uncommon in commercial fields. They are very vigorous and give a high yield of good quality cotton. Nevertheless, plants of later generations are so rare in the field as to be of no importance either commercially or from the point of view of the risk of breakdown of the species barrier. In cultures of  $F_2$  and later generation hybrids many of the plants are morphologically unbalanced, feeble and unproductive; and those that are normal and fertile segregate in the same way in the next generation, giving a majority of unproductive or partially sterile offspring. The original isolation which facilitated speciation was geographical (see Part III), but with the extended distribution resulting from seed exchange among agricultural communities, geographical isolation has gone, and the species distinction is now maintained by a very real genetic isolation in spite of free intercrossing and the production of vigorous, productive, fully fertile  $F_1$  hybrids.

It might be suggested that the interfertile cotton species should only be given sub-specific rank since their separation differs in degree and not in kind from that between varieties. Silow (1944b) has shown, however, that the separation between these interfertile species is likewise different in degree only, and not in kind, from the difference between species giving highly sterile  $F_1$  hybrids. It therefore appears reasonable to accord specific rank to all groups whose integrity is maintained by a real genetic barrier, whether this operates by preventing crossing, causing sterility in the  $F_1$  hybrid, or by leading to genotypic disintegration in later generations. Moreover, the drawing of the species boundaries to coincide with the limits of the groups within which genetic harmony exists has provided a simple and rational interpretation of plant breeding data and brought order into the previous taxonomic confusion of the genus. It is indeed remarkable that in such variable material as the commercial cottons, satisfactory morphological criteria are almost always available for the separation of the groups regarded on genetic grounds as true species.

This conception of the genetic nature of species differences is similar to that of Clausen, Keck and Hiesey (1939), and their system of classification into coenospecies, ecospecies, and ecotypes is closely parallel to the arrangement in **Sections**, species, and varieties here adopted for *Gossypium*.



## V. NOMENCLATURE

REVISION of the classification of a genus including cultivated plants inevitably leads to difficulties with nomenclature. Early classifications were of necessity based solely on morphological characters, and highly variable crop species were consequently split up under a number of names that have no significance in a natural taxonomic scheme. The original descriptions and type specimens only represent small sections of the natural group as determined by studies of field populations and genetic material. Consequently the use of any of the established specific names to cover the varied assemblage of forms now included in a crop species involves the extension of the definition far beyond the intention of the original author. Nevertheless, such an extension in meaning is the only alternative to coining a completely new set of names, and agreement should be possible between taxonomists and economic botanists in the nomenclature of crop plants if the valid name according to the International Rules of Botanical Nomenclature is accepted wherever it is not positively misleading. This principle has been adopted in selecting the names used below. Departures from current usage, and terms which must be regarded as *nomina confusa*, are discussed under the species concerned.

## VI. THE GENUS 'GOSSYPIMUM'

THE genus *Gossypium* may be described as follows: Haploid chromosome number 13 or 26. Annual *sub-shrubs*, perennial *shrubs* or small *trees*. *Branches* terete or slightly angled, tomentose, hairy or glabrous, of two kinds, monopodial vegetative branches and sympodial fruiting branches, the latter sometimes reduced to jointed peduncles or flowering spurs. The whole *plant* irregularly dotted with black oil glands. *Bracteoles* 3, usually foliar and persistent, sometimes small, or minute, rarely caducous. *Calyx* cup-shaped, truncate, undulate or 5-pointed. *Stamens*  $\infty$ , the lower parts of the filaments united into a tube, the upper free, bearing unilocular *anthers*. *Styles* clavate or furrowed, rarely divided at the tip. *Ovary* 3—5-locular, ripening to a dry, brittle, loculicidally dehiscent capsule. *Loculi* with seeds indefinite (rarely 2 only). *Seeds* covered with one or two coats of long unicellular hairs, or in some wild species almost naked.

Since related groups are likely to possess similar genetic potentialities, a good deal of parallelism between the **Sections** in interspecific variation is to be expected. Such homologous variation is in fact very pronounced, and makes the compilation of a dichotomous key impossible. In its place is given a tabular statement of the more important diagnostic characters by which the **Sections** may be distinguished (page 15).

In the following account Watt's *Gossypium bakeri* has been omitted from consideration. In the opinion of the present author, the type, which is the only specimen known, cannot be regarded as a *Gossypium*, and may be readily distinguished from all true members of the genus by the calyx cup, which is more than half-cut into 5 ovate-acute lobes, instead of being truncate.

## KEY TO THE SECTIONS

<i>Capsule and Seed Hairs</i>	<i>Stem and Leaf Covering</i>	<i>Fruiting Branches</i>	<i>Leaf Lobing</i>	<i>Bracteole Shape and Toothing</i>	<i>Androecium</i>	<i>Section</i>
Capsules with hairs on the sutures, seeds naked or fuzzy, never linted.	Glaucous.	2-∞-jointed sympodia	Lobed or entire.	Ovate entire.	—	I. <i>Sturtiana</i> .
	Glabrous or nearly so, not glaucous.	Jointed peduncles or flowering spurs.	Entire or nearly so.	Reduced, or ovate and caducous.	—	II. <i>Erioxyla</i> .
	Hairy.	2-∞-jointed sympodia.	Entire.	Many toothed.	—	III. <i>Klotzschiana</i> .
	Glabrous or nearly so, not glaucous.	∞-jointed sympodia.	Lobed.	Entire or 3-toothed, sometimes reduced.	—	IV. <i>Thurberana</i> .
	Hairy.	Jointed peduncles or 2-∞-jointed sympodia.	Lobed.	Linear, usually 3-toothed.	—	V. <i>Anomala</i> .
Capsules without hairs on the sutures, seeds linted.	Hairy or nearly glabrous.	2-∞-jointed sympodia.	Usually lobed. Rarely with both	Usually gashed or serrate. leaves and bracteoles entire.	—	VI. <i>Stockiana</i> .
	Variously hairy or nearly glabrous, not glaucous.	∞-jointed sympodia.	Lobed.	Entire, coarsely toothed or serrate, teeth rarely thrice as long as broad.	Anther filaments 'short, all about the same length Anther filaments long, upper ones longer than the lower.	VII. <i>Herbacea</i> .
				Coarsely toothed or serrate, teeth more than thrice as long as broad.	—	<i>G. tomentosum</i> in VIII. <i>Hirsuta</i> . VIII. <i>Hirsuta</i> .

## VII. THE SPECIES OF 'GOSSYPIMUM'

AMONG the most important diagnostic characters in *Gossypium* are the shape of the leaf and bracteole, the type of androecium, and the size and shape of the capsule. Drawings have been made by Mr. F. Whitburn of these characters on all species of which living material is available in the Cotton Research Station collection.<sup>1</sup> They are reproduced at half natural size in Plates I and II and IV—IX.

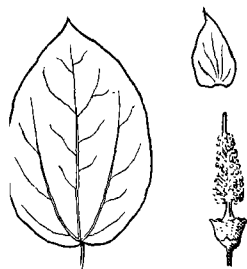
**Section I Sturtiana.** Lintless species with entirely glabrous and glaucous stems and leaves, and  $n=13$  chromosomes. Wild in Australia. 1. *sturtii*, 2. *robinsonii*. *G. robinsonii* has only been collected twice and has never been grown experimentally. *G. sturtii* is cytogenetically widely separated from all other  $n=13$  chromosome cottons (Skovsted 1937, Webber 1939, Stephens 1944d). It will cross with many other species of *Gossypium*, however, giving sterile hybrids, and in addition it is the only *Gossypium* that will graft with *Thespesia populnea*.

Leaves entire, broadly ovate      1. *sturtii*

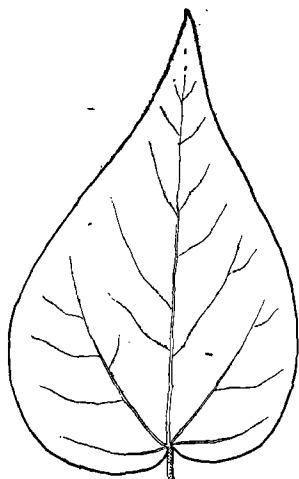
Leaves deeply 3-lobed      2. *robinsonii*

1. *G. STURTII* von Mueller (1863W, nomen illegit.) Skovsted (1935a). Plate I. *Sturtia gossypoides* R. Brown (see W), *G. australiense* Todaro (1863 W), *Cienfugosia gossypoides* Hochreutiner (1902 W), *G. gossypoides* (R. Br.) Gardner (1931). Von Mueller's (1863 W) name is invalidated by the fact that he cited Brown's earlier name, but did not take it up. Gardner (1931) attempted to establish Brown's name as *G. gossypoides*, but it had by then been applied to a Mexican plant (see below) and is therefore invalid. Todaro (1863 W) published *Gossypium australiense* for this species, but later abandoned it as a synonym of *G. sturtii* von Mueller, and quoted Sturt's material on which Brown's description was based. As *G. sturtii* is the name by which the

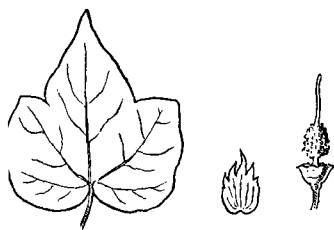
<sup>1</sup> The living collection of types of *Gossypium* maintained at the Cotton Research Station, Trinidad, will be referred to as 'the C.R.S. collection',



G. STURTII



G. ARIDUM



G. HARKNESSII



G. ARMOURIANUM



G. THURBERI

F. WHITBURN

plant is generally known, and there can be no possible confusion in its use, it seems best to establish it, on von Mueller's (1863 W) description.

Haploid *chromosome* number 13. Handsome perennial *shrub* about 3 m. tall, with many slender vegetative branches. *Stems* slender, round, developing a mauve anthocyanin pigment. The whole *plant* glabrous, covered with a bluish waxy bloom. *Fruiting branches* 2— $\infty$ -jointed. *Leaves* broadly ovate, about 6 cm. x 5 cm., very slightly cordate, apiculate, 3—5 veined. *Stipules* small, falcate, persistent, sometimes remaining after the leaves have dropped. *Bracteoles* ovate-acute, about 2.5 cm. long x 1 cm. broad, entire, free or very slightly united at the base, persistent. *Flowers* very ornamental, mauve, with a deeper mauve spot at the base of the petals. *Staminal column* long, antheriferous throughout. *Anthers* closely arranged on short filaments. *Filaments* all about the same length. *Stigmas* united throughout. *Capsules* about twice as long as broad, acute, usually 4—5-locular, the sutures bearing a line of hairs projecting between the two rows of seeds. *Seeds* 4—6 per loculus, covered with a very short, greenish fuzz.

*Distribution:* Central and South Australia, from Alice Springs to Broken Hill.

2. *G. ROBINSONII* von Mueller (1863 W). *Cienfugosia robinsoni* Hochreutiner (1902 W), *Notoxylinon robinsoni* Lewton (1915). Perennial *shrub* about 2 m. tall, with many slender vegetative branches. The whole *plant* glabrous, with a bluish waxy bloom. *Leaves* deeply 3-lobed. *Bracteoles* ovate-acute, entire, free, or very slightly united at the base, persistent.

*Distribution:* Until recently, only known from von Mueller's original collection. Recollected by Gardner in 1932 from the district between the Ashburton and Fortescue rivers in Western Australia.

**Section II Erioxyla.** Lintless species with reduced fruiting branches and  $n = 13$  chromosomes. Wild in Southern California and on the Pacific coast of Mexico. 3. *aridum*, 4. *armourianum*, 5. *harknessii*.

a. Leaves entire—b.

b. Leaves acuminate, longer than broad.

3. *aridum*.

bb. Leaves rounded or acute, as broad as long.

4. *armourianum*.

aa. Leaves shallowly 3-lobed.

5. *harknessii*.

3. *G. ARIDUM* (Rose & Standley) Skovsted (1935b). Plate I. *Cienfugosia palmeri* Rose (1890), *Erioxylum palmeri* Rose & Standley (1909), *Erioxylum aridum* Rose & Standley (1909). Haploid chromosome number 13. Large shrub or small tree, 2—6 m. tall, with long, flexible, upright branches. Twigs and young leaves minutely puberulent. Fruiting branches usually reduced to single flowered, leafless spurs 0.5 cm. long or less. Leaves entire, only slightly cordate, long acuminate, 10 cm. long or more on well-grown material. Stipules small, linear, caducous. Bracteoles very small (about 3 mm. long), triangular, persistent. Flowers pink, forming a narrow tube, 4—5 cm. long. Staminal column long, antheriferous throughout. Filaments short or fairly long, longer above than below. Stigma lobes united to the top. Capsules narrowly ovate acute, very prominently gland-dotted, 3-locular, with a few fine hairs along the inner margins of the sutures, usually 4 or 5 seeds per loculus. Seeds long and narrow, densely fuzzy.

Rose and Standley (1909) made two species, *E. palmeri*, a shrub collected in shady woods near Colima, Mexico, and *E. aridum*, a small tree common on dry hills of the coastal zone of Sinaloa, Mexico, between Mazatlan and Culiacan. The two are distinguished as follows (Standley 1923):

*E. palmeri*: Shrub. Leaves 5—12 cm. long. Calyx with 5 triangular acuminate lobes. Pedicels 10—15 mm. long.

*E. aridum*: Shrub or tree. Leaves 1.5—3 cm. long. Calyx obscurely repand-dentate. Pedicels 2—5 mm. long.

The type in the C.R.S. collection was received as *E. aridum* and was from Mazatlan, Sinaloa, Mexico. It is a large shrub or small tree, reaching a height of 7 m. in three or four years. The leaves on the young vigorously growing shoots are large, as in *E. palmeri*, and as the tree grows older they get smaller, eventually matching the description of *E. aridum*. The calyx is 5-pointed, agreeing with Standley's description of *E. aridum* and Rose's (1890) original description of *E. palmeri* ('calyx cup-shaped, 4 lines long, with 5 small acute or acuminate teeth'). The pedicel is not more than 0.5 cm. long. On young plants the spur occasionally develops into a single-jointed sympodium.

I am indebted to Dr. R. A. Silow for a drawing of a fruiting branch on a specimen of *E. palmeri* in the Gray herbarium, which shows a 2-jointed sympodium with a flower and a bud. This is similar to, but rather greater than, the sympodial development observed on young plants of *E. aridum* in the C.R.S. collection. On the whole the comparison of living with herbarium material leads to the conclusion that *E. palmeri* is only a young, and well grown, phase of *E. aridum*.

*Cienfugosia palmeri* Rose (1890) is the older name, but in *Gossypium*, Watt's *G. palmerii* has priority. Skovsted's combination *G. aridum* therefore stands.

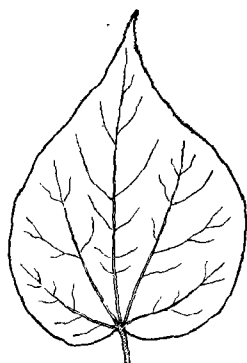
*Distribution:* Coastal zone of Sinaloa, south to Colima, Mexico.

4. *G. ARMOURIANUM* Kearney (1933). Plate I. Haploid chromosome number 13. Spreading *shrub* about 1 m. tall, with many thin, weak, drooping branches. *Twigs* and young *leaves* glabrous. *Fruiting branches* single-jointed, with a terminal, upright flower on a long pedicel, and one leaf, rarely fully developed, usually reduced to a small linear caducous appendage with two small linear caducous stipules. *Leaves* entire, rounded, not cordate, 2—2.5 cm. long, often broader than long, thin, not leathery. *Stipules* minute, caducous very early. *Bracteoles* minute, 2—5 mm. long, caducous long before anthesis. *Flowers* yellow, cup-shaped, about 2.5 cm. long. *Staminal column* short, antheriferous above only. *Filaments* short, upper ones rather longer than the lower. *Styles* long, *stigmas* joined to the top. *Capsules* rather longer than broad, rounded or prominently shouldered, very prominently dotted with black oil glands, usually 3-locular, hairs on the sutures few and small, 1—4 seeds per loculus. *Seeds* with a coat of closely appressed fuzz hairs.

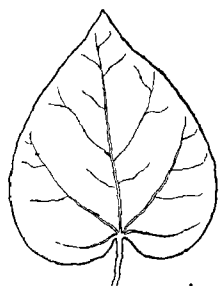
*Distribution:* San Marcos Island, Gulf of California.

5. *G. HARKNESSII* Brandegee (1899 W). Plate I. Haploid chromosome number 13. Upright *shrub*, with many strong, ascending branches, 1—2 m. tall. *Twigs* and young *leaves* minutely pubescent. *Fruiting branches* single-jointed, 1—2 cm. long, usually leafless, bearing a terminal flower. *Leaves* deeply cordate, distinctly, but very shallowly, three-lobed, leathery. *Stipules* small, linear, caducous. *Bracteoles* 1—2.5 cm. long, ovate, entire or with two or three teeth at the apex, caducous about the time of anthesis. *Flowers* yellow, bell shaped, about 3 cm. long. *Styles* long, *stigmas* joined to the top. *Staminal column* short, antheriferous above only. *Filaments* short. *Capsules* nearly spherical,

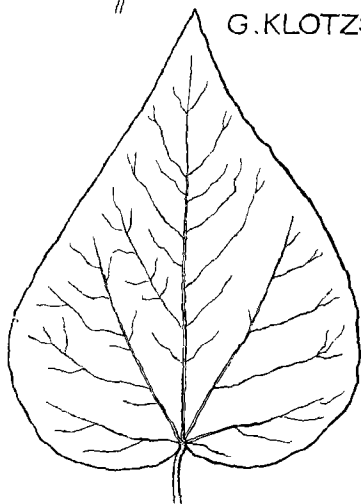




G. KLOTZSCHIANUM



G. KLOTZSCHIANUM VAR. DAVIDSONII



G. RAIMONDII

copiously ciliate on the sutures. *Seeds* covered with a silvery grey fuzz.

*Distribution:* Islands and coasts of the Gulf of California.

**Section III Klotzschiana.** Lintless species with many-jointed fruiting branches, entire leaves, and  $n=13$  chromosomes. Wild in western Mexico, the Galapagos Islands, and Peru. 6. *klotzschianum*, 6b. var. *davidsonii*, 7. *raimondii*.

a. Bracteole teeth long acuminate—b.

b. Bracteole teeth 10—15, capsule nearly twice as long as broad. 6. *klotzschianum*.

bb. Bracteole teeth 6—10, capsule round.

6b. *klotzschianum* var. *davidsonii*.

aa. Bracteole teeth long linear, almost threadlike.

7. *raimondii*.

6. *G. KLOTZSCHIANUM* Andersson (1853 W). Plate II. Haploid chromosome number 13. Perennial *shrub*, up to 4 m. tall. *Twigs*, *leaves*, and *bracteoles* softly tomentose. *Fruiting branches* 2— $\infty$ -jointed. *Leaves* entire, broadly ovate, scarcely cordate, acuminate, large, those on the main stem usually 10 cm. or more long. *Stipules* small, linear, caducous very early. *Bracteoles* cordate, with about 15 long acuminate teeth on the upper margin. *Flowers* large, about 5 cm. long, pedicel not clavate. *Styles* short, *stigmas* united to the top. *Staminal column* long, antheriferous throughout. *Filaments* short, all about the same length. *Capsules* fusiform, almost twice as long as broad, tapering above to a rather blunt tip, usually 4-locular with about 6 seeds per loculus, sutures bearing a line of fine hairs projecting between the two rows of seeds. *Seeds* frec, with a thin coat of very short fuzz hairs.

*Distribution:* Endemic in the Galapagos Islands.

6b. var. *DAVIDSONII* (Kellogg) var. nov. Plate II. *G. davidsonii* Kellogg (1873 W). Haploid chromosome number 13. Perennial much branched *shrub*, usually less than 2 m. tall. *Leaves* entire, occasionally 2- or 3-lobed, ovate cordate acuminate, not large, usually not more than 8 cm. long. *Bracteoles* cordate, with about 6—10 acuminate teeth along the upper margin. *Flowers* small, about 3 cm. long. *Capsules* almost spherical, mucronate, with 3—5 loculi, sutures bearing a line of hairs projecting between the two rows of seeds, usually 5 seeds per loculus. *Seeds* often connate, with a thin coating of closely appressed, short fuzz hairs.

*Distribution:* Shores of the Gulf of California, and the Revilla Gigedo Islands.

Watt (1907) expressed 'grave doubt' as to whether *G. klotzschianum* and *G. davidsonii* are specifically distinct. The main difference is in size. *G. klotzschianum* is a large leaved, large flowered, tall shrub or small tree and var. *davidsonii* is a small leaved, small flowered, much branched, comparatively low growing shrub. The reduction of *G. davidsonii* to varietal rank is supported by the results of hybridization experiments. It crosses readily with *G. klotzschianum*, giving a full complement of normal seeds in the hybrid capsules. First, second, and third generation hybrid plants are normal and fully fertile. The range of segregation in  $F_2$  covers the interval between the parental types, but does not extend beyond them.

7. *G. RAIMONDII* Ulbrich (1932). Plate II. Haploid chromosome number 13. Perennial shrub 2—3 m. tall, densely tomentose on all young parts, stems becoming naked with age. *Fruiting branches* 1— $\infty$ -jointed, leafy. *Leaves* entire, cordate, acuminate, large, those on the main stem usually 15 cm. or more long. *Stipules* small, attenuate acuminate, caducous early. *Bracteoles* small, broad at the base, but not cordate, cut into 15 or more very long, almost threadlike, tails along the upper margin. *Flowers* very large, 8 cm. or more long, pedicel clavate. *Staminal column* very short, antheriferous at the top only. *Filaments* long, those at the top of the staminal column longer than those below, *anthers* arranged regularly, but not in ranks. *Styles* very long, *stigmas* united to the top. *Capsules* tapering, acuminate, 3—5 locular, sutures bearing a line of hairs projecting between the two rows of seeds, 4—8 seeds per loculus. *Seeds* free, covered with a dense, irregular coat of greenish hairs, up to 10 mm. long.

Boza and Madoo (1941) have studied the distribution, morphology and relationships of *G. raimondii*. They have given excellent Plates, including two of original collections of the species by Raimondi. They concluded that morphologically *G. raimondii* resembles *G. klotzschianum*, but on its crossing behaviour they grouped it with the species here placed in the **Sections II Erioxyla** and **IV Thurberana**. The cyto-genetic relationships of the American wild species are discussed in detail in Part II. It is sufficient here to state that there is nothing in the crossing behaviour of *G. raimondii* that is inconsistent with the view here

adopted on morphological grounds that it is best included with *G. klotzschianum* in **Section III**.

*Distribution:* Departments of Cajamarca and La Libertad, north Peru.

**Section IV Thurberana.** Lintless species with 3—7-lobed leaves and acute or acuminate, entire, or rarely 3-toothed, bracteoles. Chromosome number where known  $n=13$ . Wild in Arizona and Mexico. 8. *thurberi*; 9. *trilobum*; 10. *gossypioides*.

A very imperfectly known **Section** of the genus. The present state of knowledge, and the synonymy of the group, have been discussed by Kearney (1937). From the various descriptions, three apparently distinct species can be recognized, though only very scanty material is available of two of them. *G. thurberi* from Arizona is the only species that is well known and has been studied in experimental culture.

a. Bracteoles scarcely cordate, triangular acute or acuminate—b.

b. Bracteoles triangular acute, much shorter than the petals. 8. *thurberi*.

bb. Bracteoles long acuminate, as long as the petals.

9. *trilobum*.

aa. Bracteoles cordate, broadly ovate, acute, shorter than the petals. 10. *gossypioides*.

8. *G. THURBERI* Todaro (1878). Plate I. *Thurberia thespesioides* A. Gray (1854).<sup>1</sup> Haploid chromosome number 13. Perennial, much branched *shrub* 1—3 m. tall. *Twigs* and young *leaves* sparsely covered with minute hairs, appearing practically glabrous. *Fruiting branches* many-jointed. *Leaves* deeply palmatisect into 3—7 long lanceolate acuminate lobes, on lateral branches often lanceolate acuminate entire by the suppression of the lateral lobes. *Stipules* small, narrow linear, caducous very early. *Bracteoles* small (about 1 cm. long), free, narrowly acute, entire. *Flower* an open shallow cup, petals 25—30 mm. long. *Staminal column* short, antheriferous throughout. *Filaments* intermediate in length, *anthers* loosely arranged. *Stigmas* joined throughout. *Capsules* ovate mucronate, usually 3-sometimes 4-locular, sutures

<sup>1</sup> Kearney (1937) points out that the transfer of *T. thespesioides* is invalidated by the publication of *G. thespesioides* von Mueller for the Australian plant now transferred to *Notoxylinon thespesioides* Lewton.



PLATE IIIA

*G. trilobum*. Photograph of Sessé and Moçino's type specimen of *Ingenhouzia triloba* DC. in the Madrid herbarium. ( $\times \frac{2}{3}$  approx.).



PLATE IIIb

*G. trilobum*. Photograph of Pavon's type specimen of *G. lanceaeforme* Miers  
in the British Museum ( $\times \frac{2}{5}$  approx.).

bearing a copious line of hairs projecting between the two rows of seeds, usually 6 seeds per loculus. *Seeds* angular, very finely hairy.

*Distribution*: Arizona, U.S.A.; and Sonora and south western Chihuahua, Mexico.

9. *G. TRILOBUM* (DC.) Kearney (1937). Plate III. *Ingenhouzia triloba* De Candolle (1824), *G. lanceaeforme* Miers (Britten 1893). *Shrub*, finely tomentose on the younger parts. *Leaves* approximately  $\frac{3}{4}$ -cut usually into 3 lobes. *Bracteoles* ovate cordate, long acuminate, entire (rarely 3-toothed), about 2.5 cm. long. *Flowers* small, about the same length as the bracteoles. Only known from Sessé and Moçino's types of *Ingenhouzia triloba* (in the Madrid herbarium) and Pavon's type of *G. lanceaeforme* (in the British Museum). Comparison of photographs of the two types (Plate III) leaves no doubt that they are of the same species. Sprague (1926) states that 'some Mexican plants in the Kew herbarium and British Museum marked "Herb. Pavon" were apparently collected by Sessé and Moçino', so it is probable that the two collections were made in the same area.

*Distribution*: Mexico. According to Sprague (1926) Sessé and Moçino collected in central and southern Mexico, mostly between the latitudes of Tampico and the Isthmus of Tehuantepec.

10. *G. GOSSYPIOIDES* (Ulb.) Standley (1923). *Selera gossypoides* Ulbrich (1913). *Shrub*, slightly tomentose on the young parts. *Leaves*  $\frac{1}{2}$ — $\frac{4}{5}$ -cut into 3 lobes. *Bracteoles* ovate cordate, acute, entire or rarely 3-toothed, united below, 2.5—3.0 cm. long. *Flowers* about twice as long as the bracteoles. *Capsules* ovate, mucronate, 3- or 4-locular. *Seeds* compressed, angular, very finely hairy.

The leaves of the type material are about  $\frac{1}{2}$ -cut, but two specimens with leaves approximately  $\frac{4}{5}$ -cut appear to belong to this species. They are G. B. Hinton's 5,133 from Acatitlan, in the Kew herbarium, and J. G. Ortega's 6,033 from El Carrizo, Sinaloa, in the U.S. National Herbarium (No. 1,209,600) in Washington.

*Distribution*: Oaxaca and southern Sinaloa, Mexico.

**Section V Anomala.** Fuzzy seeded, lintless species with linear, entire or 3-toothed bracteoles, and conspicuously hairy leaves. Chromosome number where known  $n=13$ . Wild in dry areas

in South-West Africa, on the southern borders of the Sahara, in Eritrea and Somaliland, and in Southern Arabia. 11. *triphyllum*, 12. *anomalum*, 13. *areysianum*.

a. Leaves divided to the base, lobes narrow.

11. *triphyllum*.

aa. Leaves  $\frac{1}{3}$  to  $\frac{4}{5}$ -palmatifid, lobes broad—b.

b. Leaf lobes ovate-acute or acuminate, constricted at the base.

12. *anomalum*

bb. Leaf lobes broadly deltoid.

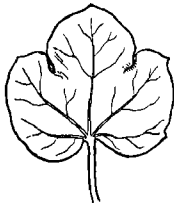
13. *areysianum*.

11. *G. TRIPHYLLUM* Hochreutiner (Ref. 2.). *Cienfugosia triphylla* Harvey (see Harvey and Sonder). Perennial shrub. Stems and leaves covered with a whitish tomentum. Fruiting branches 1- or 2-jointed, with 3 small bracts (representing a reduced leaf and two stipules) at each node, bearing one (rarely two) flowers. Leaves divided to the base into 3 narrow, tapered lobes. Bracteoles linear-acute, entire, rarely toothed. Capsules about twice as long as broad, prominently shouldered, beaked, usually 3-locular, sutures bearing a few hairs, each loculus containing only 2 almost basal ovules. Seeds bearing a single coat of fine brown hairs up to 10 mm. long.

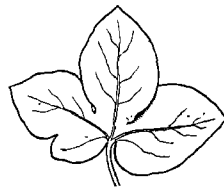
*Distribution:* South-West Africa from southern Angola to Damaraland.

12. *G. ANOMALUM* Wawra & Peyritsch (1860). Plate IV. *Cienfugosia anomala* (Wawra) Gurke, *Cienfugosia pentaphylla* K. Schum., *Gossypium herbaceum* L. var. *steudneri* Schweinf., *Gossypium senarensense* Fenzl., *Gossypium microcarpum* Welwitsch. Haploid chromosome number 13. Upright, perennial shrub with few branches, 1—2 m. tall. Stems thin and weak. The whole plant thickly covered with long, soft hairs. Fruiting branches 2— $\infty$ -jointed. Leaves  $\frac{3}{4}$ — $\frac{4}{5}$ -cut into 3—5 broad, deeply constricted lobes. Stipules small, linear, caducous. Bracteoles linear, usually divided into 3 or 4 teeth at the apex, rarely entire. Flower funnel-shaped. Staminal column long, antheriferous throughout. Stamens often arranged in 5 ranks, filaments very short. Stigmas united to the top. Capsules about twice as long as broad, beaked, dotted with prominent black glandular pustules, usually 3-locular, the sutures developing a partial false septum at the base of the capsule, and bearing a fringe of hairs above; usually 4—6 seeds per loculus. Seeds long and thin, with a single coat of fine brown hairs up to 10 mm. long.

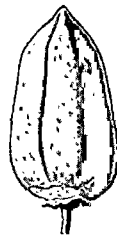
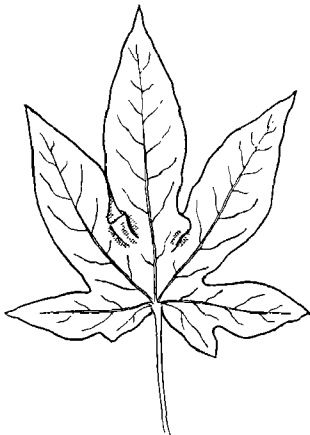
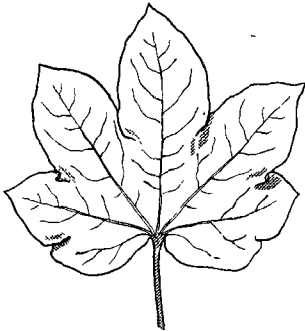




G. STOCKSII



G. ANOMALUM



G. ARBOREUM

*Distribution:* South-West Africa, Angola, French Sudan, French Equatorial Africa (Lake Chad), Kordofan, Eritrea, and Somaliland.

13. *G. AREYSIANUM* (Deflers) *comb. nov.* *Fugosia areysiana* Deflers (1895). Small *shrub*, c. 50 cm. tall, shortly pubescent on the upper parts. *Fruiting branches* 1—4-jointed, with the leaves at the nodes reduced to stipule-like bracts. *Leaves* cordate below, divided above into 3 broadly deltoid lobes. *Bracteoles* free, narrow, oblong-cuneate, generally 3-dentate at the apex, half as long again as the calyx. *Calyx* truncate, remotely 5-dentate. *Stigmas* united to the top, clavate. *Capsule* 3-locular, globose, shortly apiculate, smooth, nigro-punctate, usually 2—3 seeds per loculus. *Seeds* (imperfectly matured) oblong, covered with a short, yellowish, tenacious wool. (From Deflers' [1895] Latin description of *Fugosia areysiana*.)

*Distribution:* Only known from Deflers' original collection, of which he says: 'Collected on the southern slopes of the rocky mountains of el-'Areys (Bilad Fodhli) at 700—800 m. alt., in the month of April, when flowering and fruiting were coming to an end. Journey of 1893, Exs. No. 1,058.' Jebel el-'Areys is a mountainous coastal range in Southern Arabia, apparently about 60 or 70 miles east (and somewhat north) of Aden.

**Section VI Stocksiana.** Fuzzy seeded lintless species with ovate, usually many-toothed, bracteoles. Chromosome number where known  $n=13$ . Wild in Sind, south eastern Arabia, and Somaliland. 14. *stocksii*, 15. *somalense*.

a. Bracteoles clawed at the base and divided along the upper margin into long radiating teeth.

14. *stocksii*.

aa. Bracteoles somewhat cordate at the base, usually serrate along the upper margin, rarely entire.

15. *somalense*.

14. *G. STOCKSII* Masters (1874 W). Plate IV. Haploid chromosome number 13. Sprawling *sub-shrub*, with many thin, procumbent branches. *Twigs* and young *leaves* very finely puberulent, almost glabrous to the naked eye. *Fruiting branches* 2— $\infty$  jointed. *Leaves*  $\frac{1}{2}$ -cut into 3—5 lobes. *Leaf lobes* rounded and deeply constricted at the base. *Stipules* small, linear, caducous. *Bracteoles* free at the base, clawed, rather longer than broad, gashed into

7—10 long radiating teeth. *Staminal column* antheriferous throughout. *Stamens* comparatively few, *filaments* short. *Stigmas* united to the top. *Capsules* small, round, prominently gland dotted, usually 3-locular, sutures bearing a copious line of hairs which project between the two rows of seeds, usually 2 or 3 seeds per loculus. *Seeds* not much longer than broad, covered with a single coat of rusty brown hairs up to 7 mm. long.

*Distribution:* Sind and south-east Arabia.

15. *G. SOMALENSE* (Gürke) *comb. nov.* *Cienfugosia somalensis* Gürke (1902-4), *C. ellenbeckii* Gürke (1902-4), *C. bricchettii* Ulbrich (1912-13), *Gossypium paolii* Mattei (1916), *G. benadirensis* Mattei (1916). Upright, spindly *shrub*, up to 1.5 m. tall. *Stems* thin and weak. *Twigs* and *leaves* canescent or pubescent. *Fruiting branches* 2—4-jointed, with the leaves at the nodes reduced to small appendages no larger than the stipules, usually only bearing a single flower. *Leaves* very slightly cordate, very shallowly cut into 3 acute lobes, sometimes entire. *Stipules* small, linear, caducous. *Involucral bracteoles* ovate, cordate, shallowly serrate along the upper margin, rarely entire. *Staminal column* antheriferous throughout. *Anthers* compactly arranged on short filaments which are all about the same length. *Stigmas* united to the top. *Capsules* small (c. 1 cm. long), gland-dotted, rounded, mucronate or prominently pointed, 3—4-locular, sutures bearing a line of hairs below, only 2 basal ovules per loculus. *Seeds* long and narrow, bearing a copious coat of short, rusty brown hairs.

*Distribution:* British and Italian Somaliland, south to the Tana River, Kenya. Only two specimens are available in the Kew herbarium, Gillett's 4,507 from Biji, British Somaliland, which was labelled *Cienfugosia ellenbeckii* after comparison with Gürke's type in Berlin, and Sampson's 35 from the region of the Tana River in Kenya.<sup>1</sup>

The differences between *C. somalensis* and *C. ellenbeckii* in Gürke's original descriptions are quite insignificant, and *G. somalense* appears to be the more appropriate name to adopt in uniting them and transferring them to *Gossypium*. Mattei's *G. paolii* and *G. benadirensis* and Ulbrich's *Cienfugosia bricchettii* do not differ from Gürke's species in any important particular.

<sup>1</sup> Dr. R. L. Knight reports that he has found *G. somalense* on Gebel Merkhayat, near Omdurman, Anglo-Egyptian Sudan, and has received specimens of it from Fada, in Northern French Equatorial Africa.

**Section VII Herbacea.** Linted species with bracteoles entire, coarsely-toothed or serrate, the teeth rarely thrice as long as broad. Anther filaments short, all about the same length. Chromosome number  $n=13$ . Wild and cultivated throughout the tropics and sub-tropics of the Old World. 16. *arboreum*, 17. *herbaceum*, 17b. var. *africanum*, 17c. var. *acerifolium*.

a. Bracteoles closely investing the flower, longer than broad, entire or with 3—4 coarse teeth near the apex. Capsules tapering. 16. *arboreum*.

aa. Bracteoles flaring widely from the flower, usually broader than long, the upper margin usually serrated into 6—8 teeth. Capsules rounded, or with prominent shoulders—b.

b. Plants glabrous, or with scattered hairs on the young parts—c.

c. Leaf lobes scarcely constricted at the base.

17. *herbaceum*.

cc. Leaf lobes deeply constricted at the base.

17b. *herbaceum* var. *africanum*.

bb. Plants covered with a dense, even coat of long hairs.

17c. *herbaceum* var. *acerifolium*.

16. *G. ARBOREUM* Linnaeus (1753 W). Plate IV. The type is the specimen in the Linnean herbarium labelled '3. *G. arboreum*' in Linnaeus's own handwriting. It is figured by Watt (1907 Pl. 7c.). The Linnean specimen labelled '5. *barbadense*' is also a form of *G. arboreum*. The species as here described includes: *G. arboreum* L. and its varieties, *G. obtusifolium* Roxb., *G. nankin* Meyen and its varieties, *G. soudanense* Watt, and *G. anomalum* Watt, as interpreted by Watt (1907, 1926 and 1927); *G. indicum* Tod., *G. neglectum* Tod., *G. sanguineum* Hassk., *G. intermedium* Tod., *G. obtusifolium* Roxb., *G. cernuum* Tod., and its var. *sylhetensis* Gammie, as interpreted by Gammie (1907); and *G. herbaceum* L. var. *perrieri* Hochreutiner (1926). Haploid chromosome number 13. Perennial much branched *shrubs* up to 2 m. tall, or annual *sub-shrubs* with few or no vegetative branches, 50 cm.—1.5 m. tall. *Vegetative branches* (when present) ascending, thin and flexible. *Twigs* and young *leaves* very finely puberulent, canescent or hairy. *Fruiting branches* 2— $\infty$ -jointed. *Leaves*  $\frac{2}{3}$ — $\frac{4}{5}$ -cut into 5—7 lobes, often with small accessory lobes in the sinuses; lobes ovate oblong or curvilinear, acute, slightly constricted at the base. *Stipules* linear or falcate, caducous. *Bracteoles* closely

investing the bud and flower, more or less triangular, usually longer than broad, entire or with 3 or 4 coarse teeth near the apex; teeth rarely as much as thrice as long as broad. *Staminal column* long, antheriferous throughout. Anther *filaments* short. *Styles* short. *Stigmas* united, rarely divided at the tip. *Capsules* tapering, profusely pitted, with prominent oil glands in the pits, usually 3-, rarely 4-locular, opening widely when ripe; sutures devoid of hairs; 6—17 seeds per loculus. *Seeds* usually with two coats of hairs, short fuzz hairs and long lint hairs, occasionally with lint hairs only. (There also exist rare mutant types devoid of lint.)

Hutchinson & Ghose (1937b) made three varieties, separating the wild and primitive cultivated perennial types (var. *typicum*) from the more recent cultivated annual types (var. *neglectum*), and isolating the big-bolled annual ecotype of the Assam and East Bengal hill tracts as var. *cernuum*. They also showed that the development of the annual var. *neglectum* from its perennial ancestors had occurred in a number of geographical races characteristic of widely separated areas. Recent work by Silow (1944b) has shown that the genetic differences between the geographical races of *G. arboreum* are much greater than those between perennial and annual types of the same race. The separation of *neglectum* from *typicum* is therefore of little value to the plant breeder. To the taxonomist it is inconvenient because the distinction cannot be detected on most of the material with which he has to work. It may therefore be discarded.

The separation of *G. arboreum* into geographical races gives recognition to genetic differences of great importance in practical cotton breeding. Each race is morphologically highly variable, and though it would usually be possible to determine the one to which a representative assemblage of types belonged, no accurate classification can be made of particular strains without information on their origin and genetic behaviour. It is proposed, therefore, to make no formal taxonomic subdivision of *G. arboreum*, but to accept Silow's six geographical races as representing the best natural subdivision of the species.

*Distribution*: a. race *burmanicum*: Burma and parts of east Bengal and Assam, Indo-China, Malaya and the East Indies as far as Timor Laut. b. race *indicum*: Peninsular India from Orissa southwards. c. race *bengalense*: northern and central India from Bihar to the North-West Frontier Province, and south to

the northern districts of the Hyderabad State. d. race *cernuum*: Assam and East Bengal. e. race *soudanense*: The Sudan region of North Africa from Dahomey to Somaliland, and south on the east coast to Dar-es-Salaam, occasionally in Portuguese East Africa and Angola; southern Arabia and Aden, Madagascar. f. race *sinense*: China as far north as Manchuria; Korea, Japan and Formosa.

For details see Silow (1944b).

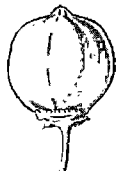
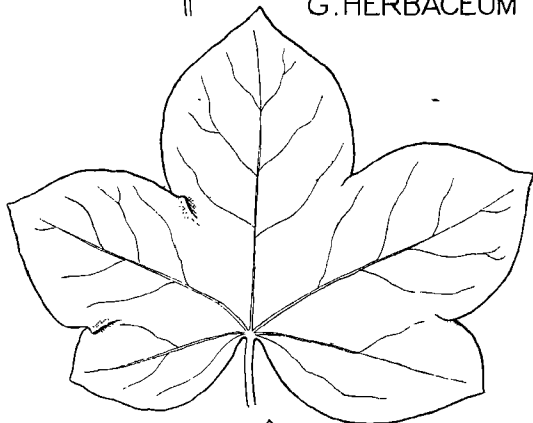
17. *G. HERBACEUM* Linnaeus (1753 W). Plate V. Watt (1907) has discussed and figured (1907 Pl. 24A) the Linnean type ('*G. herbaceum* ex Hort. Upsala') and given reasons for interpreting it as covering what he calls 'the Levantine species'. His interpretation is accepted here. Haploid *chromosome* number 13. *Sub-shrubs* usually 1—1.5 m. tall, with few or no vegetative branches. *Stems* thick and rigid. *Twigs* and young *leaves* usually sparsely hairy, rarely glabrous. *Fruiting branches* many jointed. *Leaves* usually flat,  $\frac{1}{2}$ -cut or less into 3—7 lobes; lobes ovate rotund to rounded, usually only slightly constricted at the base, without accessory lobes between the main lobes. *Stipules* small, linear, caducous. *Bracteoles* flaring widely from the flower and capsule, rounded or broadly triangular, usually broader than long, cordate, margin serrated into 6—8 broadly triangular teeth. *Staminal column* antheriferous throughout. *Anther filaments* short. *Styles* short. *Stigmas* usually united throughout, rarely cleft at the top. *Capsules* rounded, rarely with prominent shoulders, beaked, 2.0—3.5 cm. long, surface smooth or very shallowly dented, with few oil glands, 3- or 4-locular, usually only opening slightly when ripe, sutures devoid of hairs, not more than 11 seeds per loculus. *Seeds* usually bearing two coats of hairs, long lint hairs and short fuzz hairs, in rare types bearing lint only.

*Distribution*: Asia Minor through Central Asia to Chinese Turkestan, south to Baluchistan; South-Eastern Europe, and coasts and islands of the eastern Mediterranean.

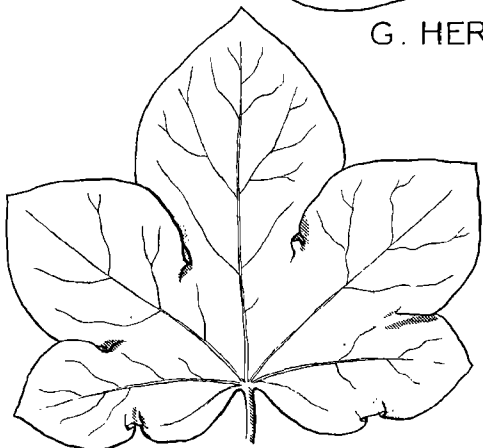
17b. var. *AFRICANUM* (Watt) Hutchinson & Ghose (1937b). Plate V. *G. obtusifolium* var. *africana* Watt (1907), *G. africanum* and its var. *bracteatum* Watt (1926), *G. transvaalense* Watt (1926), *G. simpsoni* Watt (1926), and *G. abyssinicum* Watt (1926). Haploid *chromosome* number 13. Bushy *shrub* with many thin vegetative branches, glabrous or finely tomentose on the young parts. *Leaves* thin, flat, with lobes rounded, deeply constricted at the



G. HERBACEUM VAR. AFRICANUM



G. HERBACEUM



G. HERBACEUM VAR. ACERIFOLIUM

base; sinuses between the lobes open. *Capsules* small, rounded, opening widely when ripe.

*Distribution:* Bushveld regions of South Africa from Bechuanaland to Moçambique. Intermediate types between this and var. *acerifolium* occur in the savannah regions of west and north central Africa (Chevalier 1936).

17c. var. *ACERIFOLIUM* (Guill. et Perr.) Chevalier (1939). Plate V. *G. herbaceum* L. var. *frutescens* Delile (1813) (*nomen nudum*), *G. wightianum* Todaro (1877 W), *G. obtusifolium* Roxb. var. *wightiana* Watt (1907), and *G. herbaceum* and its varieties of Gammie (1907). The Linnean specimen labelled '4 *G. hirsutum* Suratt' is of this variety. The nomenclature of the variety is in some confusion. Hutchinson & Ghose (1937b) used the *nomen nudum* *G. herbaceum* var. *frutescens* in the belief that it had been properly published. Chevalier (1939) then proposed *G. herbaceum* var. *acerifolium* from Guillemin & Perrottet's (1830) *G. punctatum* var. *acerifolium*. Their description is quite uncritical, and according to Chevalier, who has seen their material, covers *G. herbaceum* var. *africanum* as well as Watt's var. *wightiana*. The name is accepted here in the restricted sense in which Watt (1907) used the name var. *wightiana*. Haploid chromosome number 13. *Shrub* up to 2 m. tall with 0—10 strong, ascending vegetative branches. *Stems, petioles, pedicels* and *leaves* densely hairy. *Leaves* thick, rumpled, with the lobes slightly constricted at the base and the sinuses thrown up in folds. *Capsules* almost parallel sided with prominent shoulders, opening widely when ripe, or rounded, opening slightly when ripe.

*Distribution:* Kathiawar, Gujerat, and parts of the Deccan and Madras Presidency in India; and in Africa, the Sudan tract from Nubia to Senegal, Zambesia, Shire and Lake Nyasa.

**Section VIII *Hirsuta*.** Linted species with  $n = 26$  chromosomes, (a) having triangular bracteole teeth less than thrice as long as broad, and long anther filaments, the upper being longer than the lower. Wild in the Hawaiian islands. 18. *tomentosum*, (b) having bracteoles with long acuminate teeth, the teeth more than thrice as long as broad. Wild and cultivated in the New World. Introduced and acclimatized in almost all cotton growing countries of the world. 19. *hirsutum*, 19b. var. *punctatum*, 19c. var. *marie-galante*, 20. *barbadense*, 20b. var. *brasiliense*, 20c. var. *darwinii*.



Before giving a key to this **Section** it is necessary to point out that though the identification of the species should offer no difficulty, the separation of varieties on herbarium material will frequently be troublesome. The fundamental varietal differences in *G. hirsutum* are differences in growing period and fruiting habit, which are not always shown on dried specimens. In *G. barbadense* the varieties are best distinguished by differences in the size and shape of the capsules, which are difficult to preserve.

a. Staminal column short. Anthers loosely arranged, anther filaments longer above than below. Capsule surface smooth.—b.

b. Bracteole teeth triangular, less than thrice as long as broad. 18. *tomentosum*.

bb. Bracteole teeth long acuminate, more than thrice as long as broad.—c.

c. Annual sub-shrubs with few or no vegetative branches. Stems usually green or brown. Bracteoles usually having about 7—12 teeth. Anthers rather irregularly arranged on short to medium filaments. Capsules rounded, large, only faintly nigro-punctate.

19. *hirsutum*.

cc. Perennial shrubs, usually with many vegetative branches.—d.

d. Early flowering shrubs branching freely from the base, soon forming a bush without a predominant main stem or trunk, rarely small almost annual sub-shrubs. Stems and petioles usually red or reddish brown. Bracteoles usually 7—12-toothed. Anthers rather irregularly arranged on short to medium filaments. Capsules rounded, often markedly nigro-punctate.

19b. *hirsutum* var. *punctatum*.

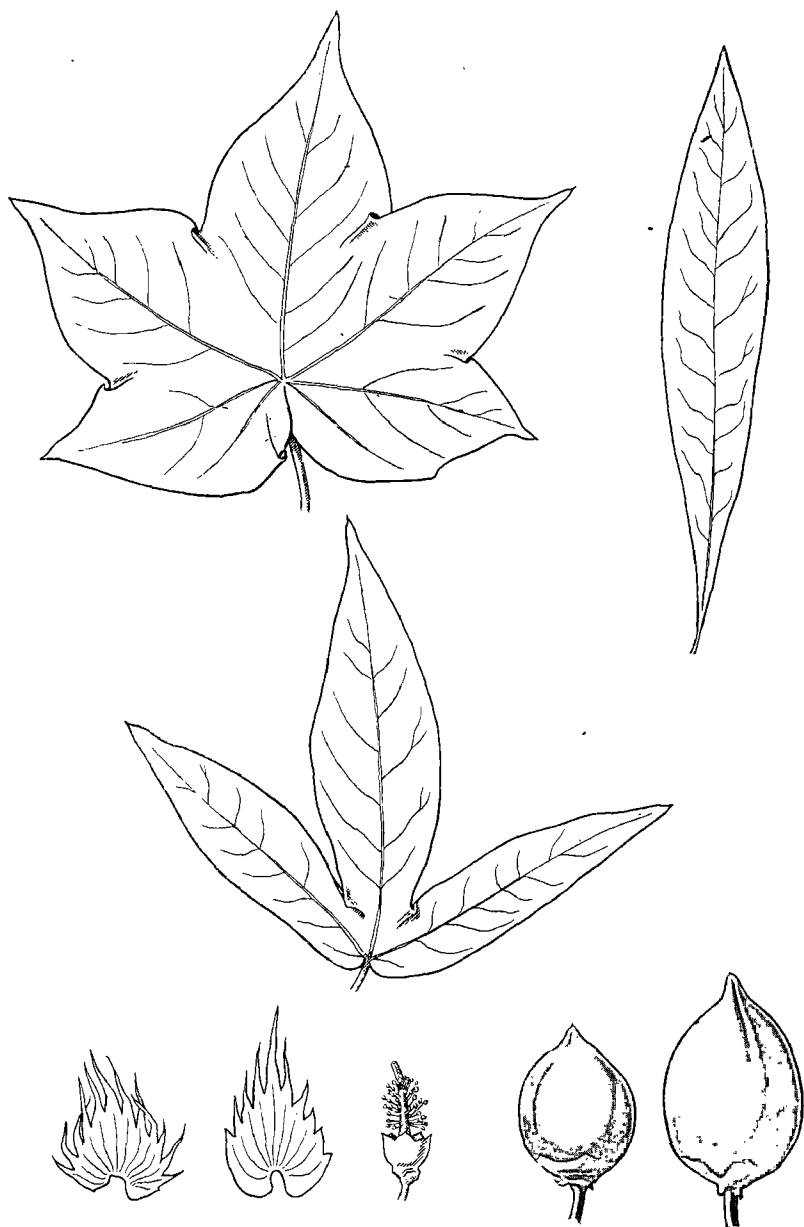
dd. Late flowering shrubs or small trees, almost always (except when ratooned low) having a definite main stem or trunk. Vegetative branches usually ascending. Stems usually green or brown. Bracteoles usually 4—7-toothed. Anthers regularly arranged on long filaments. Capsules usually tapering, only very faintly nigro-punctate.

19c. *hirsutum* var. *marie-galante*.

- aa. Staminal column long. Anthers compactly arranged, on short filaments which are all about the same length—f.
- f. Capsules usually large (3.5 cm. or more long); capsule surface usually coarsely pitted, or rarely finely pitted, with black oil glands in the pits. Seeds bearing a copious and even coat of lint—g.
- g. Capsules usually less than 6 cm. long, broadest near the base. Seeds free.
  - 20. *barbadense*.
- gg. Capsules usually more than 6 cm. long, broadest near the middle and tapering to the base. Seeds connate (kidney seeded).
  - 20b. *barbadense* var. *brasiliense*.
- ff. Capsules small (3 cm. long or less); capsule surface finely pitted with oil glands in the pits, almost smooth to the naked eye. Seeds bearing a scant irregular coat of lint.
  - 20c. *barbadense* var. *darwinii*.

18. *G. TOMENTOSUM* Nuttall (1865 W). Plate IX. *G. sandwicense* Parlatores (1866 W). Haploid *chromosome* number 26. *Shrub* 1—1.5 m. tall, the whole plant densely and very finely tomentose, having a characteristic dust-coated appearance. *Fruiting branches* many jointed. *Leaves*  $\frac{1}{2}$ -cut or less into usually 3, rarely 5, lobes; *leaf lobes* divergent, broadly ovate, almost triangular, acute; sinuses between the lobes open. *Stipules* linear, about 10 mm. x 1 mm., caducous. *Bracteoles* ovate oblong, slightly cordate, serrate along the upper margin into 8—10 coarse teeth; teeth rarely as much as thrice as long as broad. *Corolla* widely expanding, sulphur yellow, shiny, with no anthocyanin spot at the base of the petal. *Staminal column* short, antheriferous throughout. *Anthers* loosely arranged. *Upper filaments* long, lower short. *Styles* long, *stigmas* united throughout. *Capsules* 3-locular, small, tapering, with rather prominent shoulders and an acute tip; surface smooth, prominently but rather sparsely gland dotted, sutures devoid of hairs, usually 2—4 seeds per loculus. *Seeds* densely covered with brown or rusty red hairs. *Seed hairs* varying from very short fuzz hairs to lint hairs up to 10 mm. long, not readily separable into two layers and strongly adherent to the seed.

*Distribution*: Endemic in the Hawaiian islands 'growing on arid, rocky or clay plains not far from the sea' (Degener, 1933).

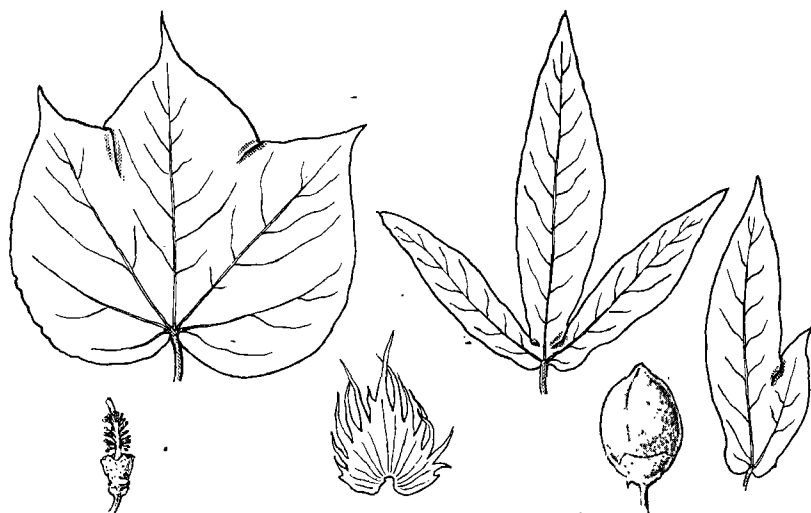


G. HIRSUTUM

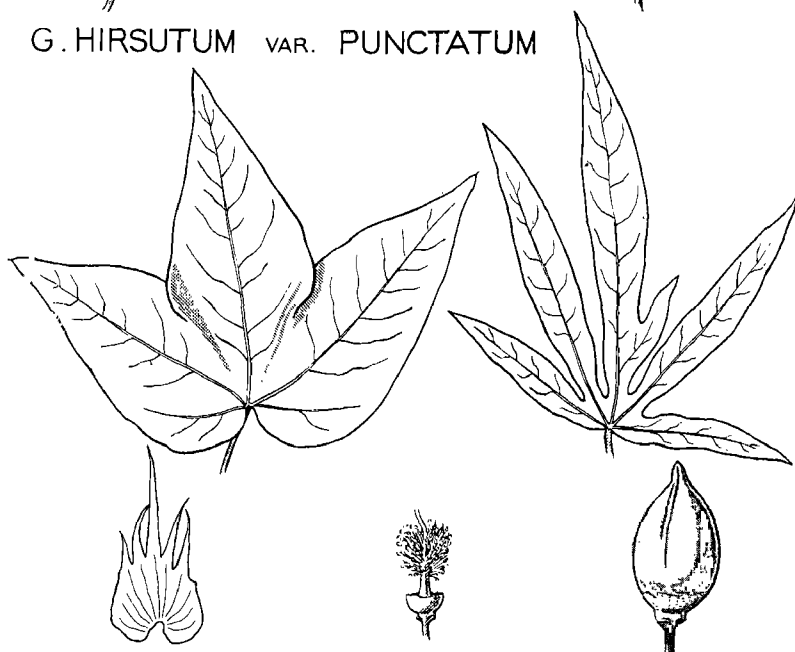
19. *G. HIRSUTUM* Linnaeus (1753 W). Plate VI. The type is Miller's specimen in the herbarium of the British Museum. It is figured by Watt (1907, Pl. 29A). The specimen labelled '*hirsutum*' in the Linnean herbarium is not this species. Includes *G. mexicanum* Todaro, *G. schottii* Watt (1907) (in part) and *G. paniculatum* Blanco (1837). Haploid chromosome number 26. Small annual sub-shrub 1—1.5 m. tall, with few or no vegetative branches. Stems usually green or brown. Twigs and young leaves varying from glabrous to densely hairy. Fruiting branches many jointed. Leaves large, cordate,  $\frac{1}{2}$ -cut or less into 3—5 lobes (in rare types  $\frac{4}{5}$ -cut into lanceolate acuminate lobes, or very rarely narrowly lanceolate acuminate entire); leaf lobes broadly triangular acuminate, not constricted, but not or only slightly overlapping at the sinuses; lateral lobes divergent, tapering to the cordate base. Stipules falcate, not more than 4 mm. wide, about 10 mm. long, caducous. Bracteoles longer than broad, cordate, gashed into usually between 7 and 12 long acuminate teeth which are more than thrice as long as broad. Flowers large. Corolla widely expanding, usually longer than the bracteoles. Staminal column short, antheriferous throughout. Anthers loosely arranged, the upper filaments ascending, usually longer than the lower. Stigmas usually united throughout, rarely divided at the tip, never separated or spreading. Capsules large, rounded, with few inconspicuous oil glands sunk beneath the smooth surface, 3—5-locular, sutures devoid of hairs, usually 5—11 seeds per loculus. Seeds bearing a copious coat of lint hairs, and usually a thick coat of fuzz hairs also.

*Distribution*: Central America from Guatemala northwards, and the Cotton Belt of the Southern U.S.A.. Introduced and acclimatized in almost all cotton growing countries of the world.

19b. var. *PUNCTATUM* (Schumacher) *comb. nov.* Plate VII. *G. religiosum* Linnaeus (1767 W), *G. tricuspidatum* Lamarck (1786 W), *G. purpurascens* Poiret (1811 W), *G. racemosum* Poiret (1811 W), *G. punctatum* Schumacher (1829 W), *G. nigrum* var. *punctatum* Webb (1849 W), *G. hirsutum* var. *religiosa* Watt (1907). Includes *G. taitense* Parlatore (1866 W), *G. fruticosum* Todaro (1877 W), *G. lanceolatum* Todaro (1877 W), *G. schottii* Watt (1907) (in part), *G. palmerii* Watt (1907), *G. nervosum* Watt (1927), and *G. morrillii* Cook and Hubbard (1926a). There can be no doubt that it was to this variety that Linnaeus (1767 W) gave the name *G. religiosum*. The Linnaean type (figured by



G. HIRSUTUM VAR. PUNCTATUM



G. HIRSUTUM VAR. MARIE-GALANTE

Watt, 1907, Pl. 32) is extremely characteristic. The commonly accepted name is *G. punctatum* Sch., and on this Webb (1849 W) established the variety *G. nigrum* var. *punctatum*. In varietal rank therefore, var. *punctatum* has priority over Watt's (1907) var. *religiosa*. Watt's (1907) *G. punctatum* var. *jamaica* also belongs to this variety, though Hutchinson (1943b), reporting recently on an extensive survey of Jamaican cottons, states that var. *punctatum* was only found in a single plot grown from introduced seed. Both wild and commensal or door-yard types are, however, known from Cuba, Haiti, and Puerto Rico. *G. purpurascens* and *G. racemosum* were described from Puerto Rico, and from an examination of present day material in the field, Hutchinson (1944) has been able to show that they are synonymous with this variety. Haploid chromosome number 26. *Shrubs* 1—3 m. tall, branching freely from near the base, and soon forming a rounded shrub with no marked trunk or main stem. (Some acclimatized African types are small annual shrubs with few, or no vegetative branches.) *Stems* and *petioles* usually red or reddish brown. *Twigs* slender. *Twigs* and young *leaves* glabrous or variously hairy. *Fruiting branches* many jointed. *Leaves* usually small, cordate, less than  $\frac{1}{2}$ -cut into 3, rarely 5 lobes (in rare types  $\frac{4}{5}$ -cut into lanceolate acuminate lobes, very rarely narrowly lanceolate acuminate entire), often ovate acuminate entire on the fruiting branches; *leaf lobes* usually broad, almost triangular, acuminate, not constricted, but not, or only slightly, overlapping at the sinuses; lateral lobes ascending, broad at the base, so that the leaf is almost parallel-sided (sometimes long acuminate, when the leaf is usually 5-lobed and the lobes are somewhat divergent). *Stipules* falcate, not more than 4 mm. wide, about 10 mm. long, caducous. *Bracteoles* triangular, cordate, gashed into usually 7—12 long acuminate teeth which are more than thrice as long as broad. *Flowers* small. *Corolla* forming a narrow tube. *Staminal column* short, antheriferous throughout. *Anthers* loosely arranged. *Filaments* short, the upper ones ascending, and usually longer than the lower. *Stigmas* united throughout, or rarely divided at the tip, never separated or spreading. *Capsules* small, rounded, with few, often almost hidden, sometimes conspicuous, oil glands sunk beneath the smooth surface, 3—4-locular, sutures devoid of hairs, usually 5—11 seeds per loculus. *Seeds* bearing lint, and usually fuzz also (Hutchinson [1944] has reported a rare type from Puerto Rico with lintless, naked, kidney seeds).

*Distribution:* Wild, and cultivated by indigenous peoples in Central America, the Cayman Islands, and along the Gulf coast of the United States as far as Florida and the Bahamas. It is the cotton of the Hopi Indians of Arizona. Wild in Haiti, Cuba and Puerto Rico. Formerly cultivated in the Bahamas. Acclimatized and run wild in many parts of Africa (in the C.R.S. collection there are types from Eritrea, British Somaliland, Zanzibar, Chole Island ('Tanganyika'), the Sudan and Egypt (Hindi weed), as well as an extensive series from West Africa). In West Africa it is cultivated for the native spinning industry on the southern margin of the Sahara where the climate is too rigorous for Upland cottons. Grown mixed with perennial *G. arboreum* in the Nadam crop of the Madras Presidency, India. Acclimatized and run wild in Madagascar, the Philippines, Polynesia and Northern Australia. The view that the form hitherto separated as *G. taitense* is endemic in Polynesia can no longer be maintained. Seemann (1860-1) states that no cotton is indigenous in Fiji.<sup>1</sup> Watt (1907) ascribes to *G. taitense* material collected in New Caledonia, the Philippines, and Madagascar. Two types from Haiti in the C.R.S. collection are near the Polynesian type, and recently a wild xerophytic race known as 'algodon brujo', which is indistinguishable from *G. taitense*, has been found in Puerto Rico (Hutchinson 1944). The absence of any satisfactory morphological criteria on which *G. taitense* can be separated, and the demonstration that it occurs as an indigenous wild plant within the natural range of var. *punctatum*, are sufficient grounds for regarding it as no more than an ecological race.

19c. var. MARIE-GALANTE (Watt) *comb. nov.* Plate VII. *G. barbadense* var. *marie-galante* (Watt) Chevalier (1938). Includes *G. birkinshawii* Watt (1927), *G. harrisii* Watt (1927), *G. marie-galante* Watt (1927), *G. mustelinum* Miers (ms. fide Watt 1907). The nomenclature of var. *marie-galante* has suffered from confusion in the interpretation of Poiret's (1811 W) *G. purpurascens*. Watt's (1907) Plate 44 of *G. purpurascens* is a fair representation of a *marie-galante* cotton, but the specimens he cites are mostly from areas in the Old World where var. *punctatum* is acclimatized and var. *marie-galante* is not known. According to Chevalier (1939),

<sup>1</sup> I am indebted to Mr. B. E. Parham for the information that 'the cotton plant . . . occurs nowhere in natural climax vegetation [in Fiji] but is always as recorded by Seemann, to be found adjacent to old native cultivations or to native villages—amongst secondary growth.'

Poiret's type was from tropical America, probably Puerto Rico, and Hutchinson (1944) has given reasons for believing that the name is a synonym of *G. hirsutum* var. *punctatum*. It was grown, and flowered, in Paris. This rules out var. *marie-galante*, which is photoperiodic, and does not flower in the latitude of Paris before the onset of cold weather. The name *purpurascens*, and the description 'stems purplish brown', is much more suggestive of var. *punctatum*, in which a deep reddish brown stem pigment is very common. It appears, therefore, that in ascribing the *marie-galante* cottons to *G. purpurascens*, Harland (1932a, 1939, 1940a) was misled by Watt's (1907) Plate. In any event the name must lapse, since as Chevalier (1939) has pointed out, Lamarck's (1786 W) *G. glabrum* would have priority if the type were given specific rank. In varietal rank, var. *marie-galante* is the only published name.

Haploid chromosome number 26. Large shrub or small tree 2—5 m. tall, with many large, ascending vegetative branches springing from the lower part of the main stem. Stems usually green or brown. Flowering photoperiodic, only occurring during the months with short days. Twigs and young leaves usually glabrous, sometimes sparsely hairy, rarely densely tomentose. Fruiting branches many jointed. Leaves large, cordate, sometimes  $\frac{1}{2}$ -, usually  $\frac{2}{3}$ -cut into 3, rarely 5, lobes (in rare types  $\frac{1}{5}$ -cut into lanceolate-acuminate lobes). Leaves on lateral branches very often entire, cordate-acuminate. Leaf lobes usually ovate-acuminate, rarely almost triangular with acuminate tips, usually somewhat constricted at the base, sinuses between the lobes open; lateral lobes divergent. Stipules falcate, not more than about 4 mm. wide, about 10 mm. long, caducous. Bracteoles usually narrowly triangular, cordate, gashed into usually 4—7, rarely more, long acuminate teeth, more than thrice as long as broad. Flower forming a narrow cup, very rarely widely expanding. Staminal column short, antheriferous throughout. Anthers many, regularly arranged. Upper filaments long, ascending, lower short, spreading. Stigmas united throughout, very rarely divided at the tip, never spreading. Capsules variable in size, usually rounded, tapering to an acuminate point, with few oil glands sunk beneath the surface, 3—4-locular; sutures devoid of hairs, usually 5—11 seeds per loculus. Seeds bearing a copious coat of lint hairs, sometimes having a coat of fuzz also, often without fuzz except for a minute tuft at the tip.



TABLE I  
Frequency arrays of leaf shape and number of bracteole teeth in *G. hirsutum* and its varieties.

	Sinus length / Leaf length	Total	Mean
<i>G. hirsutum</i>	0    0.01    0.06    0.11    0.16    0.21    0.26    0.31    0.36    0.41    0.46    0.51    0.56    0.61    0.66 0    0.05    0.10    0.15    0.20    0.25    0.30    0.35    0.40    0.45    0.50    0.55    0.60    0.65    0.70	— — — — — — — — — — — — — —	53
var. <i>punctatum</i>	— — — — — — — — — — — — — —	— — — — — — — — — — — — — —	37
var. <i>marié-galante</i>	— — — — — — — — — — — — — —	— — — — — — — — — — — — — —	52
			0.52
			0.53
			0.43

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Number of teeth per bracteole

	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	Mean
<i>G. hirsutum</i>	—	—	1	4	6	10	23	17	14	8	4	1	—	—	88	9.6
var. <i>punctatum</i>	—	—	—	—	1	2	4	3	10	8	2	1	—	—	31	9.8
var. <i>marié-galante</i>	1	5	19	7	12	2	4	1	1	—	—	—	—	—	52	6.1

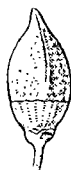
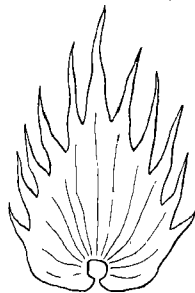
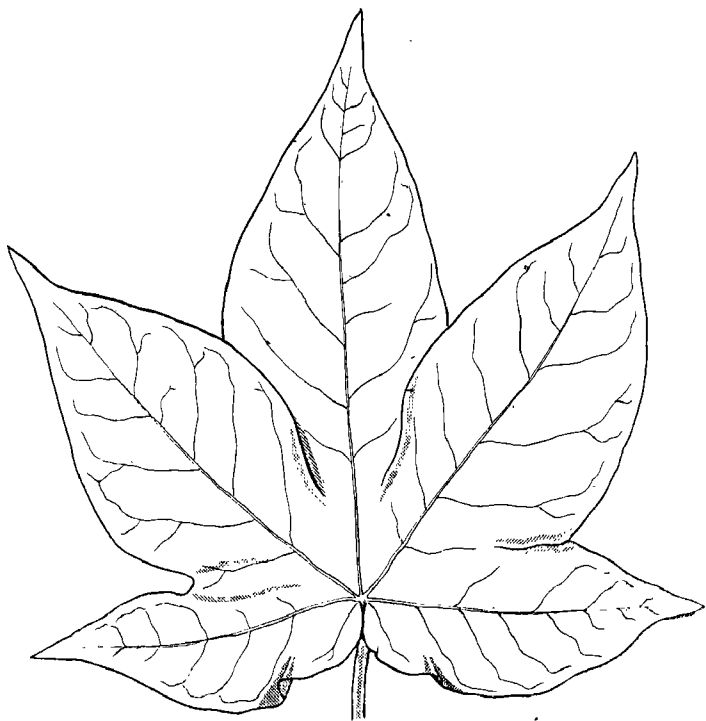
*Distribution:* Wild and cultivated in the Greater Antilles, Lesser Antilles, Ecuador, the Spanish Main, the Guianas, and northern and eastern Brazil. (The Marie-Galante<sup>1</sup> cotton of the Antilles, Moco of Brazil.) There is no record of its having been successfully introduced into North America or the Old World. The name 'Bourbon' attached to *G. purpurascens* by Watt (1907) properly belongs to the cotton acclimatized in the island of Bourbon. This true Bourbon was later introduced from there into India, and examination of the Bourbon component of the Madras Nadam crop shows that it is typical var. *punctatum*.

The determination of the most suitable rank for the groups here classified as varieties of *G. hirsutum* has been the subject of considerable discussion (Watt 1927, Zaitzev 1928, Mauer 1930, Chevalier 1938, Hutchinson 1939a, Harland 1940a). There is no doubt that each variety is well defined ecologically, genetically, and to a large extent morphologically. They are well-defined ecotypes on the classification of Clausen *et al.* (1939). Yet they are morphologically distinct chiefly in the statistical sense, that each variety is *on the average* different from other varieties in a number of characters, in almost every one of which the distributions overlap. Harland (1940a) cites leaf shape and number of bract teeth as characters on which the Upland (*G. hirsutum*) and *G. hirsutum* var. *marie-galante* (Harland's *purpurascens*) groups can be distinguished. He gives a correlation table of leaf shape and number of bract teeth in [*marie-galante*],<sup>2</sup> together with the approximate value of Upland. The range of variation in Upland is considerable, however, and frequency arrays of leaf shape and number of bract teeth in Upland, *punctatum* and *marie-galante* types in the C.R.S. collection are given in Table I to show that, although the mean values of *marie-galante* are distinct from the means of the other two varieties, yet the overlapping in both characters is too great to permit classification of individual types with certainty.

In Harland's (1940a) view 'the assemblage of [*marie-galante*] cottons is as distinct from Upland as, say *arborescens* is from

<sup>1</sup> This term, as used in West Indian agriculture and the trade, includes the produce of perennial *G. barbadense* with that of *G. hirsutum* var. *marie-galante*, which are there grown together.

<sup>2</sup> In quoting Harland, [*marie-galante*] has been substituted for 'Bourbon' to make it clear that he is discussing the assemblage of cottons here assigned to var. *marie-galante*.



G. BARBADENSE

PLATE VIII

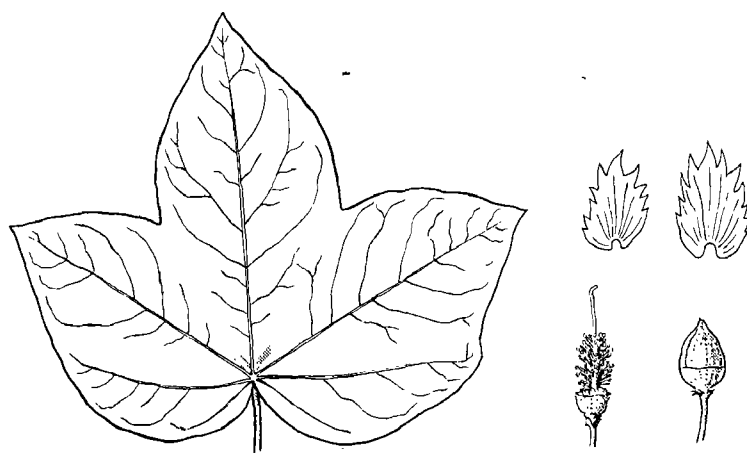
*herbaceum*'. Yet when grown in mixed culture in Madras and Kathiawar the specific integrity of *G. arboreum* and *G. herbaceum* is maintained unimpaired in spite of natural crossing. In contrast, to quote Harland (1939), 'the general tendency in regions where it [var. *marie-galante*] exists has been to introduce Upland cotton, with which it easily hybridizes, the result being the swift contamination and hopeless mongrelization of the [*marie-galante*] stock. This is what has happened in North Brazil in the States of Rio Grande do Norte and Ceara, where it is now difficult to find plants of pure [*marie-galante*] strain.' Similar evidence of free inter-breeding between Upland and *G. hirsutum* var. *punctatum* is provided by Roberty (1938), who states that commercial American varieties cultivated in the French Sudan gradually change to var. *punctatum* if bred for several generations without selection. Since var. *punctatum* has become so successfully acclimatized that it is now the common perennial cotton of the country, there can be little doubt that what Roberty ascribes to degeneration is the result of hybridization and natural selection.

Hybrids between *G. hirsutum* and its vars. *punctatum* and *marie-galante* have been made, and extensive  $F_2$  cultures grown at the Cotton Research Station, Trinidad. In both crosses the range of variation was within the limits of the parental types, and in none were unbalanced, sterile, or morphologically abnormal segregates observed. It may be concluded that to classify these three natural groups as varieties or ecotypes of a single species is in accord with all that is known of their genetics and morphology. In addition, it serves the convenience of the plant breeder, by bringing freely inter-breeding forms within the limits of a single species, and of the systematic botanist, by including in one species what he cannot always separate with confidence.

20. *G. BARBADENSE* Linnaeus (1753 W). Plate VIII. According to Watt (1907), the type is Plukenet's specimen in the British Museum, figured by Watt (1907, Pl. 46A). In the Linnean herbarium there is a sheet labelled '*barbadense?*' which is not this species. Includes *G. peruvianum* Cavanilles (1785-90 W), *G. vitifolium* Lamarck (1786 W), *G. microcarpum* Todaro (1876 W), *G. maritimum* and its var. *polycarpum* Todaro (1877 W), *G. barbadense* var. *maritima* Watt (1907 W), and *G. multiglandulosum* Philippi (1891). Haploid chromosome number 26. Perennial shrub or annual sub-shrub 1-3 m. tall, with few or many strong



G. BARBADENSE VAR. DARWINII



G. TOMENTOSUM

ascending vegetative branches. *Twigs* and young *leaves* varying from completely glabrous to densely coated with long grey hairs. *Fruiting branches* many-jointed. *Leaves*  $\frac{2}{3}$ -cut into 3—5 lobes; *leaf lobes* long, tapering, acuminate, slightly constricted at the base, the sinuses usually thrown up in folds. *Stipules* variable in size, falcate or auriculate, caducous early, or persisting for some time. *Bracteoles* almost as broad as long, cordate, gashed into usually 10—15 long acuminate teeth, which are more than thrice as long as broad. *Flowers* large, usually exceeding the bracteoles. *Corolla* not widely expanding, forming a long narrow tube.\* *Staminal column* long, antheriferous throughout. *Anthers* closely packed on short *filaments* which are all about the same length. *Stigmas* united to the top, or if cleft near the tip, never spreading. *Capsules* usually large (3.5—6 cm. long), rarely small, usually 3- sometimes 4-locular, broad at the base, usually tapering to an acute tip, sometimes prominently shouldered; surface rough, with oil glands at the bottom of pits, rarely almost smooth; sutures devoid of hairs, usually 5—8 seeds per loculus. *Seeds* free, bearing a copious and even coat of lint; beneath the lint there may be a full coat of fuzz, or a tuft of fuzz at one or both ends, or fuzz may be absent altogether.

*Distribution:* Tropical South America from the north western Argentine northwards, and the Galapagos Islands. Occasional in Central America (probably introduced). Probably recently spread throughout the Antilles. Introduced thence to South Carolina and Georgia, where annual, fine-linted types were selected and gave rise to Sea Island cotton. The Egyptian cotton of commerce is grown from annual varieties descended from hybrid stocks of Sea Island x perennial *barbadense* parentage. Introduced into Africa, India, the East Indies and Polynesia, where it is to be found sporadically in or near food gardens, and occasionally in the bush. Cultivated in Southern Nigeria (Ishan cotton).

2ob. var. *BRASILIENSE* (Macfadyen) *comb. nov.* *G. lapideum* Tussac (1818 W), *G. brasiliense* Macfadyen (1837 W). Includes *G. pedatum* Watt (1927). Haploid *chromosome* number 26. Perennial *shrub*, 2—3 m. tall, with few or many vegetative branches. *Twigs* and young *leaves* glabrous or nearly so, rarely tomentose. *Leaves* and *flowers* very large. *Capsules* very long and narrow (7 cm. or more long. See the large capsule in Plate VIII), broadest near the middle, tapered to the base. *Seeds*

connate ('kidney' cotton). The complex of characters including large leaves, large flowers, large capsules and kidney seeds, is typical of the variety. With the extension of distribution which has occurred in recent times, var. *brasiliense* has been brought into contact with typical *G. barbadense* and hybridization has followed. The *brasiliense* character complex then breaks down, and in areas of overlap such as the West Indies, various recombination products are to be found. These segregates, of which Sprague's (1914) *G. brasiliense* var. *aposperrum* may be cited as typical, do not merit taxonomic recognition.

*Distribution:* Eastern tropical South America. Now distributed throughout Central America and the Antilles, and sporadic in Africa and India.

20c. var. *DARWINII* (Watt) var. nov. Plate IX. *G. darwinii* Watt (1907), *G. purpurascens* Hooker (1847 W), *G. klotzschianum* Robinson & Green (see W), *G. barbadense* Robinson (1902 W) (in part). The type is Darwin's specimen collected on James Island during the voyage of the *Beagle* in 1835, now in the Cambridge University herbarium. Two other specimens named by Watt are in the Kew herbarium. They were collected, one by Dr. Habel during the expedition of the *Indefatigable* in 1868 and the other by Dr. Bauer (n.22) on Chatham Island in 1891 (see Watt 1907). Haploid chromosome number 26. Perennial, much branched *shrub*, 2 m. tall, branches slender and flexible. *Twigs* and young *leaves* densely and finely tomentose, and *leaves*  $\frac{2}{3}$ -cut into 3—5 tapering lobes, almost bronze in colour (typical form); or *Twigs* and young *leaves* almost glabrous, and *leaves*  $\frac{4}{5}$ -cut into 3—5 lanceolate lobes, suffused with a red anthocyanin pigment (narrow-leaved form). *Capsules* small (less than 3 cm. long) broad at the base, almost triangular in outline, with a long acute point; profusely dotted with black oil glands which are sunk in very small pits. *Seeds* free, bearing a scanty, irregular coat of short, rather fine, brown lint, which is strongly adherent to the seed, and a dense coat of brown fuzz hairs.

*Distribution:* Endemic in the Galapagos Islands.

Varietal distinctions in *G. barbadense* are much less sharp than in *G. hirsutum*. Study of the extensive range of types in the C.R.S. collection has shown that the annual and perennial forms are not sharply separated either morphologically or ecologically. The Sea Island and Egyptian cottons are therefore

included in a single taxonomic group with the varied assemblage of wild and cultivated *barbadense* cottons ranging through western South America from Colombia, through Ecuador and Peru to Bolivia and the north western Argentine. The kidney cottons of the Brazilian forests, on the other hand, form a distinct ecotype. The large leaves, large flowers, and very long boll are characteristic and they can usually be distinguished with ease from typical *G. barbadense*.

The reduction of *G. darwinii* to varietal status is also a consequence of the study of a wide range of South American types. Five types collected in the Galapagos Islands have been contributed to the C.R.S. collection by officers of the United States Department of Agriculture. Of these types, one is a typical perennial *G. barbadense*, and one is a small-bolled type with the irregular coat of brown lint of *darwinii*, but otherwise predominantly *barbadense* in appearance. Two are typical broad-leaved *darwinii* types, and one is an almost glabrous, laciniated leaved form with red anthocyanin in the leaves. The last three are closely similar in their much branched habit, slender, flexible twigs, their very small bolls, and their seeds with an irregular coat of brown lint. Dr. Silow states that in a representative collection of material from the Galapagos Islands in the Gray Herbarium, it was not possible to draw any clear line of demarcation, either morphological or geographical, between the various forms of *darwinii* and *barbadense*. It will be suggested later (in Part III) that this intergradation may be the result of hybridization between the long isolated *darwinii* and true *barbadense* recently introduced from the mainland. Whether the variability is primitive or the result of recent hybridization, it is evident that *darwinii* cannot be given more than varietal rank, and the discovery by Professor Boza in the Tumbes district of north Peru of a wild *G. barbadense* type having some resemblance to var. *darwinii* supports the conclusion that the separation between them does not go very deep.



## VIII. CONCLUSION

THE outstanding feature of the taxonomy of *Gossypium* is the way in which diversification has accompanied geographical distribution. The differentiation of the main **Sections** is associated with their distribution into the four tropical and subtropical continents. Further development was of minor importance until the invention of spinning by man, since when the two **Sections** bearing lint have had an enormous selective advantage over the rest of *Gossypium*. The vast increase in numbers in these **Sections** consequent on domestication, their introduction by man into new environments, and the particularly favourable conditions provided by cultivation for adaptive evolution under natural and human selection, have given rise to the great range of forms now found in the cultivated cottons.

### ADDENDUM

Distribution of *G. stocksii* (*See above: page 31, line 8*)

Since this report was set up in type the attention of the authors has been drawn to the fact that Glover and Gilliland have collected *G. stocksii* at Wareg in British Somaliland. (G. and G. 895 of 9.7.45 in the Amani herbarium.)

*THE EVOLUTION OF THE SPECIES OF 'GOSSYPIMUM'*

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I. INTRODUCTION

CONSIDERED from an evolutionary point of view, the outstanding feature of the genus *Gossypium* is the contrast between the wild lintless species and the cultivated cottons and their immediate relatives. The former are cytologically highly differentiated and geographically widely scattered, but the individual species are usually restricted in distribution and low in variability. They are not cottons in the true sense, since none of them have seed hairs which can be spun. The latter, all of which bear true lint on the seeds, and to which the term cottons will be restricted in what follows, are cytologically much less differentiated. Four of the five species in the group are very widely distributed throughout the tropics and sub-tropics, both in cultivation and as naturalized wild forms, and contain a vast range of intraspecific variability. It is the purpose of this paper to outline the status of the wild lintless species and to identify the major factors which governed the evolution of the cottons from them.

## II. THE WILD SPECIES

THE wild lintless species of *Gossypium* are perennial xerophytic shrubs occurring naturally in the arid regions of the tropics and sub-tropics. The commonest habitat is the beds and on the banks of creeks and streams that are dry for a large part of the year, but some species are sufficiently drought-resistant to spread to dry, rocky hillsides, or over arid stony or sandy plains. They are essentially plants of open associations, and suffer severely from heavy competition in the seedling stage, or under overhead shade. Recent studies of the status of linted cottons in Trinidad and Puerto Rico (Hutchinson, 1943c, 1944) have shown that this intolerance of competition has persisted among the cultivated species which have been developed under much more mesophytic conditions, and all cottons, even the Sea Island types established in the humid tropical conditions of the West Indian islands, withstand drought better than excessive moisture. Moreover, where formerly cultivated cottons have become established in the wild, their spread is limited to xerophytic plant communities in which there is open ground where seedlings can develop without close competition. It is evident, therefore, that the complex of characters associated with the xerophytic habit of the wild species is fundamental to the constitution of *Gossypium*, and it follows that the history of the genus is bound up with the history of the arid regions of the tropics and sub-tropics.

*Gossypium* is very widely distributed, wild species having been discovered in all the continents of the world which extend into the sub-tropical region. Cytological studies (Skovsted, 1937; Webber, 1939) have shown that all wild lintless species that have been grown in culture have  $n=13$  chromosomes, but the complement is extensively differentiated so that the species of each continent have a characteristic genom, and pairing in hybrids between species from different continents is low. The cytological evidence on the relationship of the continental groups, with which the evidence from crossing behaviour is in

agreement, has been discussed by Beasley (1942), who has devised a convenient nomenclature for the various distinct genomes. Unfortunately, only one species of each of the **Sections Sturtiana, Anomala, and Stocksiana** have been grown in culture, and Beasley's genomes can only be regarded as representing these **Sections** if it is a fair assumption that morphological similarity indicates cytogenetic affinity. Beasley assigns B to the genome of *G. anomalum*. His C genome, representing *G. sturtii*, and D, representing the American wild species, are widely distinct from the B of *G. anomalum* and from each other. The cross B x C fails in all cases. B x D can be made with difficulty and usually gives empty seeds except in the case of *G. anomalum* x *G. klotzschianum* var. *dauidsonii*, which is easily made and gives a full complement of good seeds. C x D is a difficult cross, and if successful usually gives empty seeds. The E genome, representing *G. stocksii* from Sind and Arabia, is cytologically widely distinct from B, C, and D. E x C and E x D give empty seeds in almost all cases. E x B gives good seeds which germinate and give feeble hybrid seedlings.

Evidently the continental groups which carry these widely distinct genomes must have been isolated from each other for a very long period, and in view of the fact that they are inhabitants of arid regions, and bear seeds that are not adapted to distribution over long distances by water (Skovsted, 1937), it can only be supposed that they reached their present areas by dispersal across land masses with a dry climate. To postulate land connexions with continental desert conditions uniting Africa, Asia, Australia, and America is beyond reason. A possible explanation of their present distribution is provided by Wegener's theory of continental drift. The fragmentation of a large continental land mass which he postulated fits the facts of the distribution of *Gossypium* remarkably well. Wulff (1943) has given figures (after Köppen and Wegener) of the supposed location of the continental masses from the Jurassic age onwards, with an indication of the distribution of arid regions. In the Jurassic period (Wulff's Fig. 25) the continental masses of South America, Africa, Southern Asia, and Australia all lay in a single block south of the Equator. Stretching diagonally from what was to become western Arabia to the west coast of the land mass where Peru is now located was an enormous arid tract. It is not recorded as stretching as far as Australia, but an arid area is

noted in Australia in the Cretaceous period (Wulff's Fig. 26). At that time the mass had begun to split up into continents, and arid areas are recorded in central South America, central Africa and western Arabia, south-eastern Africa and Australia (besides others in the northern hemisphere that are irrelevant to the present discussion). Three of these arid areas cover the areas of distribution of the present continental groups of *Gossypium*. The fourth, in south eastern Africa and Madagascar, covers the area now inhabited by *Gossypioides*, which is morphologically one of the closest relatives of *Gossypium*, having been

**Fig. 1**  
**Geographical Areas**  
**of**  
**American wild species of *Gossypium***

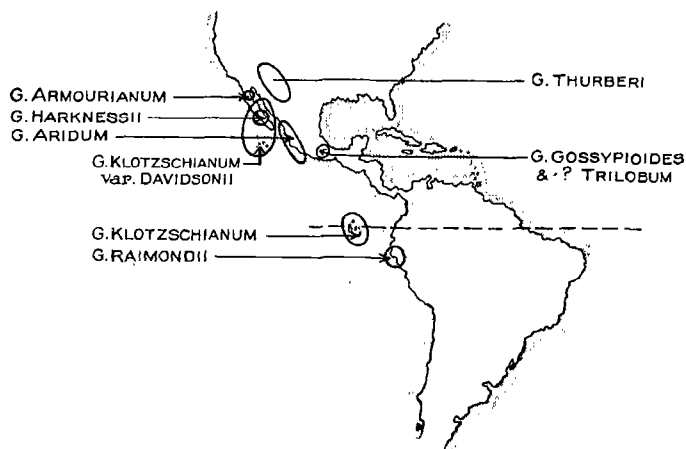


Fig. 1. Geographical areas of American wild species of *Gossypium*.

excluded from it on the results of recent cytological and physiological studies (Harland 1932a, Skovsted 1935c). If continental drift may be accepted, then, the differentiation of a primitive Angiospermous genus into the three major continental groups of species of *Gossypium* may well have taken place following the break up of the great Jurassic arid area into continental arid zones in the Cretaceous period. On this theory the central African and western Arabian arid area gave rise to two **Sections**, **Anomala** and **Stocksiana**, that are now partially 'sympatric'

(Mayr 1942) in their distribution. If future investigations show that the cytological facts are in accordance with the morphological grouping, it may be concluded that the present position is the result of convergence from formerly distinct areas situated in north central Africa and Indo-Arabia respectively.

Of the continental groups, that from America is the only one of which several species have been studied cytologically and genetically. Their relationships have been discussed by Skovsted (1937), Harland (1939), Webber (1939), Stephens (1942), and Boza and Madoo (1941). Hutchinson's division into three **Sections** on morphological grounds (see Part I above) is supported by the evidence from their geographical and ecological distribution (see Fig. 1).

The three species of the **Thurberana** are to be found along the main mountainous backbone of Mexico and the south western United States. Nothing is known of the ecological requirements of *G. gossypoides* beyond the fact that it occurs at altitudes of from 2,800 to 4,500 feet in the State of Oaxaca, Mexico, or of the origin of *G. trilobum* except that Sessé and Moçino who collected it, worked in central and southern Mexico (Sprague 1926). *G. thurberi* is well known. It is found 'at altitudes ranging from a little over 2,000 to 7,000 feet' (Coad 1915) in the arid mountain regions of south eastern Arizona, and has also been collected in Sonora and south western Chihuahua. Coad (1915), studying its distribution in south eastern Arizona, reported: 'While colonies are to be found high on the sides of the canyons and on ridges, the most common habitat in the mountains round Tucson is in the beds of the canyons and small washes. Here it grows among the rocks and on the small islands in the bed of the wash wherever there is sufficient moisture and enough protection from the force of the current in flood seasons.'

South and west of the area of *G. thurberi*, on the dry coastal hills of Sinaloa, Mexico, *G. aridum* is to be found, growing 'among stunted shrubs and trees' (Rose and Standley 1909). A single specimen has been collected as far south as Colima 'in shady woods' (Rose 1890). The specimen is somewhat off-type, and the habitat is exceptional for a wild species of *Gossypium*, and the locality should be re-examined. The other two species included with *G. aridum* in the **Erioxyla** are only known from Lower California and the islands around its coasts. *G. harknessii* was first collected on Santa Margarita Island, off the west coast of

Lower California, and has since been recorded from various localities on the east coast of the peninsula and the neighbouring islands as far north as Carmen Island (Kearney 1933). *G. armourianum* is only known from San Marcos Island, in the Gulf of California, a considerable distance north of the most northerly record of *G. harknessii*. Kearney (1933) has recorded that '*G. armourianum* . . . is very common in draws, on talus and in sandy bottoms. When the writer saw the plants there on 6 April 1931, they were flowering profusely and had many unripe capsules, although there had been no heavy rainfall at that locality for more than eighteen months. This species is, therefore, pronouncedly xerophytic like *G. harknessii*, which occurs in similar habitats.'

Of the **Section Klotzschiana**, *G. raimondii* occurs in dry coastal valleys in north Peru. According to Boza and Madoo (1941) 'it has only been found on the shores of rivers or in the beds of dry streams, streams which only flow at certain seasons of the year, and which have very little water and small slope. In stretches where the river has not a definite bed, and where it floods easily at certain times, the species has been found in compact formations' (Trans. from Spanish). It has never been found on the ridges between the valleys. *G. klotzschianum* is confined to the Galapagos Islands, where it is 'found in stony places in the lower sterile regions' (Watt 1907). Its var.  *davidsonii* is found in the Revilla Gigedo Islands, in Lower California and neighbouring islands from José del Cabo to Magdalena Bay, and on the mainland of Mexico near Guaymas. It therefore overlaps the area of *G. harknessii* in Lower California. According to Cook and Hubbard (1926b), 'In two localities near Guaymas, *G. davidsonii* was found in abundance, growing as a wild plant among other desert vegetation'. Kearney (in corres.) stated, '*G. davidsonii* . . . was observed only on the banks and in the beds of intermittent streams, and its habitat seemed less xerophytic than that of *G. harknessii*.' The two species may therefore be ecologically separated, though their geographical distributions overlap.

It will be noted that among the American wild species, with the exception of the overlap of *G. harknessii* and *G. klotzschianum* var.  *davidsonii*, both the **Sections** and the individual species are strictly 'allopatric' (Mayr 1942) in distribution, although they occupy ecologically similar habitats.

Good estimates of genetic relationships between species can only be obtained where cross pollination results in successful fertilization, since failure of fertilization may result from other factors besides general genetic incompatibility. Crosses between the species of the American wild group have been reported by Skovsted (1935a & b), Webber (1939), Hutchinson (1939b), Boza and Madoo (1941). The conclusions to be drawn from a comparison of the available information may be summarized as follows:

1. *G. klotzschianum* and its var. *dauidsonii*, which intercross freely giving a fertile  $F_1$  and a uniform and fertile  $F_2$ , cross freely with the other species of the group including *G. raimondii*, but give empty seeds only.

2. *G. raimondii*, which is placed on morphological grounds in the same **Section** as *G. klotzschianum*, crosses fairly easily with *G. thurberi* and *G. armourianum*, but most of the seeds produced were empty or only partly filled. In *G. raimondii* x *G. thurberi* only 10 per cent of the seeds germinated and produced hybrids. The  $F_1$  plants were only partially fertile (Boza 1941). None of the seeds of *G. raimondii* x *G. armourianum* germinated. Crosses with *G. harknessii* produced empty seeds, and with *G. aridum* gave only one capsule showing evidence of successful fertilization out of 34 pollinations, and this fell at 16 days.

3. *G. thurberi* crosses 'rather easily' (Webber 1939) with *G. armourianum* and *G. harknessii*, giving  $F_1$ s which are 85 per cent and 70 per cent self-fertile respectively. A small  $F_2$  of *G. armourianum* x *G. thurberi* was highly variable in both morphological characters and fertility. *G. thurberi* x *G. aridum* set about half the flowers pollinated but nearly all the seeds obtained were empty (Skovsted unpublished data). A single  $F_1$  hybrid was practically sterile when left to self, and only of low fertility when used in a backcross with the parental species.

4. *G. armourianum* only crosses with *G. aridum* with difficulty, and the  $F_1$  is very highly (but not quite completely) sterile.

5. *G. armourianum* crosses freely with *G. harknessii* giving a vigorous, fully fertile  $F_1$  and a very variable  $F_2$ , with some plants as fertile as the  $F_1$ .

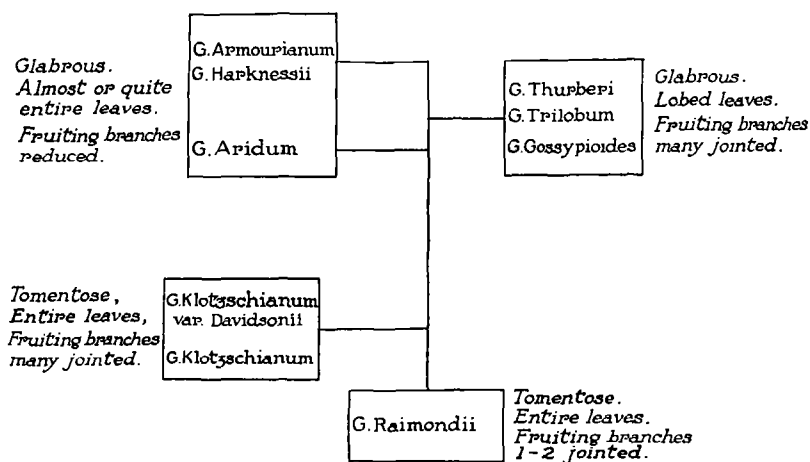
Chromosome pairing approaches 13 II in all  $F_1$ s that have been grown to flowering and examined in meiosis, so there is no evidence of gross cytological differentiation.

On all the evidence *G. thurberi* must be regarded as a central



type. Its closest relatives (apart from *G. trilobum* and *G. gossypoides* which have not been studied in culture) are *G. armourianum* and *G. harknessii*. *G. aridum* is genetically isolated, but lies nearer to *G. thurberi*, *G. armourianum* and *G. harknessii* than to *G. raimondii*. *G. raimondii* is also isolated, but appears to be a little closer to *G. thurberi* than to the other American wild species. *G. klotzschianum* and its var. *dauidsonii* are even more isolated, and only

Fig. 2  
Diagrammatic representation of  
relationships of American wild diploid species



F.W.

Fig. 2. Diagrammatic representation of relationships of American wild diploid species.

on morphological and geographical grounds can they be regarded as closer to *G. raimondii* than to the other species. The geographical, morphological and genetic relationships are summarized in the diagram in Fig. 2.

Knowledge of the other continental groups is much less complete. Of the Australian species only *G. sturtii* has been grown in culture. The distributions of the two known species are widely separated (Fig. 3). Both are plants of arid regions. The notes

'found in the beds of the creeks of the Barrier Range' on Sturt's specimen of *G. sturtii*, and 'from Warrainboo Creek' on Gardner's material of *G. robinsonii* suggests that they resemble some of the American species in growing where the severity of the climate is mitigated by occasional floods and some underground water.

Of the **Section Anomala**, only one species (*G. anomalum*) has been grown in culture. *G. triphyllum* is fairly well represented in herbaria, but so far as is known, *G. areysianum* has only been collected once, and no specimens have been available for study. The distributions of the species of **Sections Anomala** and **Stocksiana** are given in Fig 4. *G. triphyllum* occupies the south west African arid zone, and *G. areysianum* a small area in southern Arabia. *G. anomalum* covers a very wide area. It will be seen that its distribution is discontinuous. The type was collected in the south western area (Angola and South West Africa), which is separated by the Congo forest belt from the largest area of distribution of the species in the arid Sudan, Eritrea, and Somaliland. Chevalier (1933) has quoted records of habitat and ecology on specimens from the French Sudan and the French Niger Colony, of which the following are typical: 'Zone of spiny plants . . . very common in arid steppe regions,' 'the only plant growing in stony lands, eaten by camels'. So far as the localities are known, *G. anomalum* appears to be a constituent of the 'Acacia—desert grass savannah'.

*G. anomalum* is the only wild species of *Gossypium* with a continent-wide range. It is also exceptional in having a discontinuous distribution, but examination of herbarium material reveals no evidence of the establishment of distinct varieties or geographical races. While in the Sudan region it appears to be the only wild representative of the genus, in the south west it occupies the same area as *G. triphyllum*, and in Somaliland it overlaps *G. somalense*. Extensive climatic changes are known to have occurred in Africa during Pleistocene times (Moreau 1933), and as a working hypothesis, it may be suggested that the species of **Section Anomala** were differentiated in isolation, and the centrally situated *G. anomalum* subsequently spread into the areas of *G. triphyllum* and *G. somalense* during recent extensions of the arid zones in dry inter-pluvial periods. It will be necessary to reconsider the relationships between the **Anomala** and the **Stocksiana** when *G. areysianum* and *G. somalense* have been studied in culture.

Fig. 3  
Distribution of  
Australian wild species of *Gossypium*

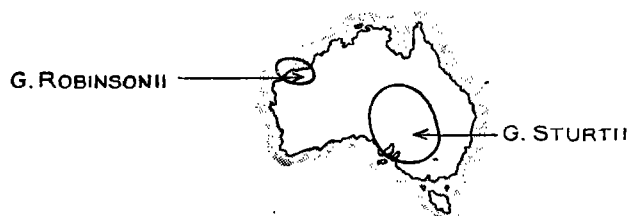


FIG. 3. Distribution of Australian wild species of *Gossypium*.

Fig. 4  
Geographical Areas  
of  
African & Asiatic wild species of *Gossypium*

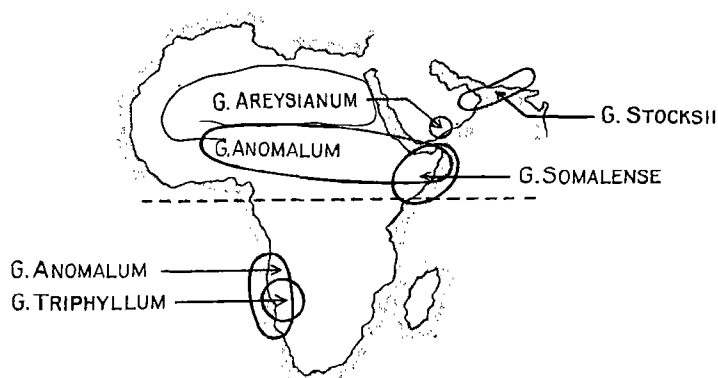


FIG. 4. Geographical areas of African and Asiatic wild species of *Gossypium*.

Of the two species of **Section Stocksiana**, *G. stocksii* is wild on the desert plains of Sind and in the Dhofar mountains of south eastern Arabia, and *G. somalense* occurs throughout Somaliland, and southwards in dry regions in northern Kenya. It has recently been collected by D. H. Kevan near El Wak on the Kenya-Somaliland border. He describes the locality as 'a low flat and soft white limestone outcrop' bearing 'an acacia-thorn bush flora with ? *Sansevieria* sp. being the main ground flora with admixture of small aloe and other semi-desert plants. Rainfall probably about 3 inches a year at the most.'

The general impression resulting from a study of the wild species of *Gossypium* is of an ancient, much differentiated sub-genus, the species of which are genetically widely separated, often replacing each other in different parts of the same ecological area, but showing little tendency to spread. So far as can be determined from herbarium material and reports of field observations, genetic variability is low, and the lower categories of differentiation are rare. Only one species (*G. anomalum*) is widely distributed. No geographical races are known. Only one species (*G. klotzschianum*) has a variety, and only one inter-specific cross (*G. harknessii* x *G. armourianum*) gives a fully fertile F<sub>1</sub>. Judging from the wild species, *Gossypium* is a stationary or receding genus made up for the most part of ancient relic species.

### III. THE ORIGIN OF THE CULTIVATED COTTONS

#### a. The Old World Cottons

ALL species of *Gossypium* have at least some seed hairs. In the wild species they may be so short as to escape notice, as in *G. klotzschianum*, *G. thurberi* and *G. sturtii*, or they may be up to 10—12 mm. long, and more or less appressed to the seed. These seed hairs vary enormously in both length and diameter, but they are all unicellular outgrowths of the epidermis of the seed, and are therefore morphologically equivalent. In the early stages of development they are thin walled. Later, cellulose is deposited within the cuticle, and gradually encroaches on the space occupied by the protoplasmic cell contents. At maturity in the wild species, the lumen is practically obliterated, and the dry seed hair on a ripe seed is long, tapered, circular in cross section, and filled with cellulose except for a small central cavity left by the drying up of the cell contents (Fig. 5a).

In lint hairs the deposit of cellulose is much less, so that at maturity a considerable lumen remains. When the capsule opens and the lint hairs dry, the cavity left by the drying up of the cell contents is so large that the hair collapses, forming a ribbon. The cellulose is deposited in spirally arranged fibrillae (Balls 1924), and the strains set up by the collapse of the cellulose-lined tube cause the ribbon to twist, giving the characteristic convolutions of cotton lint (Fig. 5b). It is these convolutions that give cotton the 'cling' that makes spinning possible, and it is the difference between the flat, spirally twisted ribbon, and the cylindrical, unconvoluted simple hair that is the essential distinction between cotton lint and the seed hairs of the wild species. All other characters, such as length, the distinction between lint and fuzz, and the number of hairs per unit area of seed coat, are secondary, and the basic problem of the origin of the cottons is that of the origin of the convoluted hair.

It will be evident from Fig. 5 that whatever else may be involved, a reduction in the amount of cellulose thickening is the

first essential if a flattened, convoluted, lint hair is to be developed from a simple cylindrical seed hair. Provided the cellulose fibrillae are laid down in the same way, a reduction

Fig. 5

Simple Seed hairs & Convoluted Lint hairs



A. Part of a normally ripened seed hair of *G. Raimondii*



B. Part of a normally ripened lint hair of *G. Barbádense*



C. Part of a dried immature hair of *G. Raimondii*

magnification  $\times c$  300

P.W

FIG. 5. Simple seed hairs and convoluted lint hairs:

- A. Part of a normally ripened seed hair of *G. raimondii*.
- B. Part of a normally ripened lint hair of *G. barbadense*.
- C. Part of a dried immature hair of *G. raimondii*.

in secondary thickening sufficient to cause collapse on drying should result in the appearance of convolutions, and the basic change from a simple seed hair to spinnable lint would be

accomplished at a single step. It is of interest to note that lint formation can be induced quite easily in *G. anomalum* and *G. raimondii* by picking capsules prematurely, and drying their contents in a desiccator. *G. anomalum* capsules normally burst about 33 days after flowering. Immature capsules were picked at 7, 13, and 15 days from flowering, the contents dried, and dried hairs teased out, mounted in liquid paraffin, and examined under the microscope. At 7 days, the hairs were unthickened, and were consequently extremely fragile, and collapsed without any sign of convolutions. At 13 days, thickening had begun in some hairs, and a few convolutions were observed. At 15 days most hairs were partially thickened, and had developed on collapsing about as many convolutions as are to be seen in normal lint hairs. These observations were repeated on *G. raimondii* seed hairs, and they also developed convolutions when picked and dried at the right time (see Fig. 5c). It may be concluded, first that the sequence of cell elongation followed by secondary thickening is much the same in simple seed hairs as in cotton lint, and secondly that the arrangement of the cellulose fibrillae is the same in both, so that the development of the flat, spirally twisted lint hairs is merely a matter of retarding the rate of secondary thickening so that the hair collapses on drying. The basic change involved in the origin of lint is therefore physiologically simple.

There is evidence that the change from simple hairs to lint hairs is also genetically simple. In 1940 Mr. W. R. E. Nanton, Cotton Officer Montserrat, collected seed from two abnormal plants, no doubt of mutant origin, in pedigree material of the MSI variety of Sea Island cotton. The produce of these plants was remarkable in that the lint remained closely appressed to the seed as in the wild species instead of fluffing out as in normal cotton, and microscopic examination showed that many of the hairs were fully thickened and unconvoluted. The increase in thickening was accompanied by about a 20 per cent reduction in length, but even so, both in length and in quantity of seed hair the mutant resembled the linted cottons, and therefore illustrates the extent to which other factors have been added to increase the quantity and quality of lint, after the basic change was established. Crosses with normal Sea Island gave a normal  $F_1$  and in  $F_2$  32 normal: 8 non-expansive. In the normal class a few plants gave seed cotton that did not fluff out fully, and

it is probable that a careful estimate of the degree of thickening would show that dominance is not complete. There can be no doubt, however, that in this material a single factor difference is responsible for the change from convoluted lint hairs to simple seed hairs.

Other single factor differences causing considerable changes in degree of secondary thickening are green lint (Neely 1943), and a very dark mahogany brown lint, both of which are associated with low cellulose deposition in New World cottons. Evidently genes having a large enough effect on secondary thickening to change the simple seed hairs of a wild species into lint hairs are not uncommon, and it is suggested that the lint of the progenitors of the cultivated cottons originated by mutation in this way.<sup>1</sup>

Comparing the great specific differentiation and generally limited distribution of the lintless species with the limited specific differentiation, great genetic variability, and enormous geographic range of the linted species, it is evident that the latter have escaped from the stationary, almost relic status of the former, and emerged into an aggressive colonizing phase that has spread them into more mesophytic habitats and across the varied climatic conditions of whole continents. With all the vast geographic extension that followed their development, there is only one external feature that constantly distinguishes the aggressive colonizers from the static species, and that is their possession of lint. Though various theories have been advanced to explain the 'function' of lint—that it is some kind of a protection to the seed, that it makes possible dispersal by birds, and so forth—there is no evidence that it is of any selective value to a cotton plant growing wild in natural vegetation. Only as a source of textile raw material to civilized man is it of any real advantage to the plant. If the linted species had been developed first, and man had adopted cottons which he found

<sup>1</sup> The belief that such a gene might cause the development of lint in a wild species is strengthened by the fact that the seed of *Gossypioides brevilandatum*, a rare wild plant from Madagascar, bears true lint, of a colour very close to that imparted by the mahogany gene in the New World cottons. So far as is known, it has never been spun. It compares unfavourably with modern cottons, but may well be as good as the form originally domesticated. Lint of this type, fully convoluted but only 12–15 mm. long, might well arise among wild species of *Gossypium* bearing simple seed hairs as a result of mutation at a locus controlling the rate of secondary thickening.



growing as established wild species, it would be expected that wild linted cottons would be found at or near the primary centres of variability of the cultivated Old World species, and would be absent from the more recent peripheral areas of their distribution. No such situation exists, wild forms of both Old World cotton species being found in all parts of their range where suitable ecological conditions exist. These wild cottons are only found where cotton is now cultivated, or is known to have been cultivated within historic times, and the wild and cultivated forms in any area are always closely related. They show every sign of being secondarily wild forms descended from escapes from cultivation, and it may be concluded that the origin as well as the distribution of the cottons is intimately connected with the utilization of their lint by man.

Since it has been shown that a primitive lint might arise by a simple genetic change in a lintless species, the way in which such a rare linted variant might have been adopted and improved by man may be considered. The spinning of the long fibres of flax and wool is known to be more ancient than cotton spinning, which, on account of its short staple length, requires a higher degree of technical skill. There can be little doubt that the discovery and improvement of cotton was made by a civilized people already well versed in the manufacture of linen and woollen fabrics. Such peoples existed in ancient times in the Nile valley, Mesopotamia, and the valley of the Indus and its tributaries. Cotton was not in use in Babylonia when Herodotus wrote in 445 B.C., however, and it only became known in the Nile valley in the Meroitic age (about 500 B.C. See Griffith and Crowfoot, 1934). The most ancient cotton fabrics known are the fragments recovered during the excavations at Mohenjodaro in Sind at levels which are dated at approximately 3000 B.C. (Gulati and Turner, 1928), and according to Sir John Marshall (quoted by Gulati and Turner, 1928), 'the Babylonian and Greek names for cotton (Sindhu and Sindon respectively) have always pointed to the Indus valley as the home of cotton growing'.

Though cotton was first used in the Indus valley, the cytogenetic evidence appears to be conclusive that the wild relatives of the earliest cultivated species are to be found among the African and Arabian *Anomala*, and not among the African, Arabian and Indian *Stocksiana*. The chromosome complements

of *G. anomalum* and the Old World cottons still retain sufficient homology to permit genetic analysis of their hybrids (Silow 1941), whereas crosses between the Old World cottons and *G. stocksii* give sterile hybrids in which chromosome homology is very low. It appears, therefore, that the progenitors of the early cottons of the Indus valley must have been introduced from southern Arabia or north eastern Africa.

Coastwise trade between north western India and the north eastern coast of Africa by way of southern Arabia is very ancient, and the first cottons, differing little from their wild lintless prototypes save in the possession of a fluffy coat of lint hairs, may well have been introduced to the Indus civilization as a curiosity. Their primitive lint, probably not much more than  $\frac{1}{2}$  inch long, and grey, brown, or rust coloured, cannot have offered much attraction to people accustomed to the long fibres of flax, but the oily seed may have been of some value, and the lint may well have been used in the first instance for lamp wicks, and as a trimming or for embroidery on linen or woollen fabrics, and only gradually have been developed as an independent textile material. (See Massey [1924] for quotations illustrating the ancient use of cotton for ornamenting linen, and as weft with a linen warp.)

The later stages of the development of cotton from an accessory of the textile craft to a major raw material no doubt took place in Sind, where the superiority of cotton over wool and flax for hot weather clothing would rapidly become apparent. The fragments discovered at Mohenjo-Daro were evidently made by competent craftsmen, and not by people experimenting clumsily with a new art, or with an unfamiliar raw material. In all hair characters that could be measured the Mohenjo-Daro cotton was within the range of Indian cottons of the present day, so it is certain that the major changes involved in the evolution of lint were complete at that time.

In this manner it may be supposed that the early civilization of north western India, which added to man's cultivated plants the bread wheats, peas and other legumes, and mustard, rape, and other oilseeds (Vavilov 1935), also gave the world the original diploid cottons. Their subsequent differentiation and the formation of the species, varieties, and geographical races which provide the bulk of the cotton crop of the Old World will be left for discussion in Part III. Here it is proposed to examine

the part played by an early diploid form in the origin of the cottons of the New World.

#### b. The New World Cottons

The relationships of the 26 chromosome complement of the New World cottons have been the object of extensive cytological studies (Skovsted 1934, 1937; Webber 1935). Skovsted showed that it consists of a set of 13 rather larger chromosomes homologous with the 13 chromosomes of similar size in the Old World cottons (Beasley's A genom), and 13 rather smaller chromosomes homologous with the smaller chromosomes of the American wild diploid species (the D genom). He showed that pairing between the chromosome complements of *G. sturtii* (the C genom) and New World cottons, *G. stocksii* (the E genom) and New World cottons, and *G. anomalum* (the B genom) and New World cottons was very low, and concluded that only from a hybrid between an Old World cotton and an American wild species could a complement homologous with the New World set be synthesized.

Genetic evidence in support of this allopolyploid constitution has been adduced by Harland and Atteck (1941). They demonstrated the existence of normal alleles of the crinkled mutant of New World cottons in the D genom of the wild American species. Similarly, of the two anthocyanin series in New World cottons, the  $R_1$  alleles are allelomorphous with those controlling anthocyanin pigmentation in the D genom of the American diploids, while the  $R_2$  alleles are allelomorphous with the extensive anthocyanin series in the A genom of the Old World cottons. Recently Silow (1946) has extended the evidence of homology by demonstrating the existence of duplicate linkage groups involving  $R_1$ —cluster on the one hand and  $R_2$ —short branch on the other, cluster and short branch being duplicate genes causing a reduction in the length of the fruiting branches. Not only is there evidence, therefore, of gene homology between the allopolyploid set and the A and D diploid sets, but both gene and chromosome duplication have been demonstrated between the A and D components within the allopolyploids.

Stephens (1942) has pointed out that the extent of multivalent formation in hybrids in which each genom is represented twice is a more sensitive index of homology than is pairing in hybrids

in which each occurs once only, since in the former case normal pairing between true homologues is possible, and any over-pairing must presumably indicate fairly close homology, whereas in the latter case in the absence of true homologues, even very low affinities may result in pairing. Skovsted's results may therefore be checked by comparison with those obtained by Harland (1940b), Beasley (1942), and at this Station on meiosis in hexaploids obtained by colchicine treatment of hybrids between New World cottons and various wild species. Beasley (1942) reported that a 2 [(AD)A] hexaploid formed by doubling a hybrid of *G. hirsutum* x *G. herbaceum* gave meiotic figures in which 'some of the chromosomes usually are in complex associations', indicating the existence of the over-pairing that would be expected on Skovsted's theory of homology between the A genom and one set of 13 chromosomes in the New World cottons. A hexaploid from *G. hirsutum* x *G. anomalum* 2 [(AD) B], on the other hand 'was nearer normal in chromosome behaviour than any other induced *Gossypium* polyploids that were studied'. Any homologies that may exist between the B genom and chromosomes of the New World set must therefore be low. Similarly, his hexaploid from *G. hirsutum* x *G. sturtii* 2 [(AD) C] sometimes gave at meiosis 39 pairs of chromosomes, 'though usually some were in associations of four, and two or more univalents may be present'. That homology between the C genom and the New World complement is low has also been confirmed by Stephens (1944d) from meiotic studies of a tetraploid hybrid of the constitution (AD) AC).

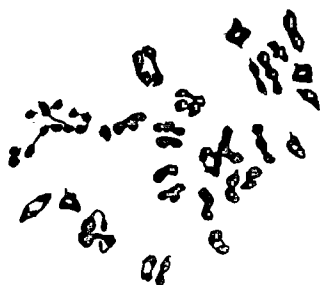
Hexaploids have been obtained from hybrids between New World cottons and five American wild species (D genom). Harland (1940b) found hexaploids involving *G. armourianum* and *G. aridum* were 'fully fertile, on both male and female sides', and that involving *G. thurberi* was 'almost fully fertile'. Beasley (1942) found that the *G. hirsutum* x *G. harknessii* hexaploid 'had a higher fertility and, therefore, apparently a more normal chromosome behaviour than hexaploids 2 [(AD) A] of American 26 and Asiatic 13 chromosome species'. In meiosis he found some associations of 3 or 4 chromosomes. It will be seen that the hexaploids involving these four American diploid species were all more fertile than the *G. hirsutum* x *G. herbaceum* hexaploid, and therefore the homologies of their D sets with the corresponding New World chromosomes must be lower than are the

A homologies. At this Station a hexaploid has been synthesized from a hybrid between *G. barbadense* and *G. raimondii*. It is practically sterile, setting only two or three seeds per season by open pollination. Examination of pollen mother cells showed that 'all bivalent' association must be extremely rare. Metaphase I in all plates seen contained several multivalents. One plate which could be analysed completely is reproduced in Fig. 6. Metaphase II plates counted varied from 34 to 42. Usually few chromosomes were left unpaired, so laggards were uncommon and tetrad counts showed 98 per cent with four microspores. It

Fig. 6

1st. Metaphase of  
Hexaploid *G. Barbadense* x *G. Raimondii*

Associations : 1 VIII , 4 IV , 5 III , 19 II , & 1 I



x c. 1600

FIG. 6. First metaphase of hexaploid *G. barbadense* x *G. raimondii*.

will be seen that the homology of the D genom of *G. raimondii* with chromosomes of the New World cottons is much closer than is that of the D sets of the other four species tested.

Beasley (1942) accepted Harland's view that the origin of allopolyploidy was in late Cretaceous or early Tertiary times. Consequently he did not expect to find more than general chromosome homologies between the allopolyploids and their nearest existing diploid relatives. He synthesized a 2 [AD] allopolyploid from a *G. arboreum* x *G. thurberi* hybrid which, though

male sterile, set seed freely when pollinated by New World cottons. In the meiosis of the resulting hybrids most of the chromosomes were paired as bivalents, but most cells had one or more multivalent associations and frequently one or two univalents. This degree of homology is as great as might be expected on the theory that allopolyploidy is of ancient origin, but the cytological evidence discussed above indicates that a tetraploid synthesized from a hybrid between an Old World cotton and *G. raimondii* may be expected to prove more closely homologous with New World cottons than Beasley's hybrid. Independent evidence in support of this conclusion is available from several sources. Stephens (1944c), has given phenogenetic data on the development of leaf shape in Old World and New World cottons, and has demonstrated the similarity in leaf development between Old World x *G. raimondii* hybrids and New World cottons. Further, in size, plant habit, shape and number of bract teeth, and flower characters, the diploid Old World cotton x *G. raimondii* hybrids resemble New World cottons much more closely than does any other AD hybrid that has been synthesized. Finally, Hutchinson, Stephens, and Dodds (1945) have shown that the seed hairs of *G. raimondii* are of a type which give convoluted hairs in hybrids with Old World cottons, whereas those of other American wild species are not.

It has been one of the major problems of the evolution of the New World cottons to discover how the two diploid parents were brought together so that hybridization could take place. Harland (1939) showed that the A and D diploids are distributed on the tropical borders of the Pacific Ocean, while the (AD) polyploids have their major centres of variability near the Pacific coasts of the American continent within the area occupied by the D diploids, or are actually endemic in Pacific islands. The discovery in Puerto Rico (by Hutchinson 1944) of the race of *G. hirsutum* var. *punctatum* hitherto referred to *G. taitense* and regarded as endemic in central Polynesia, leaves *G. tomentosum* as the only species endemic in the Pacific islands. Nevertheless, the distributions of the New World species together with the well-established fact that the diploid cottons are much more ancient in southern Asia than in Africa, leave no room for doubt that the migration of the diploid species was across the Pacific and not across the Atlantic. Further, since the New World diploids are all static or relic species with limited

distributions, whereas the Old World cottons are aggressive colonizers, and the centres of variability of the two major allopolyploids are within the area at present occupied by the American diploids, it is a fair inference that the gap was bridged by the spread of the Old World cottons, and not by an enlarged area of distribution of the American wild species.

Harland (1939) has suggested that the parental species met across a Pacific land bridge in late Cretaceous or early Tertiary times. This theory is open to objections that appear to be insuperable. It has been shown above that the distribution of the wild diploid species is in accordance with expectation on Wegener's theory of continental drift, according to which the Pacific must be a very ancient ocean. Even if it were not, however, and land bridges across it did exist in those eras, paleobotanical evidence indicates that the major sub-generic groups of flowering plants were not established before the early Tertiary, so that, allowing time for sufficient differentiation among the diploids to give allopolyploid behaviour in a hybrid, the parents of the New World cottons cannot have come together until much later than the period Harland postulated for his land-bridge.

The ecological implications of the land bridge theory appear to have been largely overlooked. The Pacific Ocean is 10,000 miles wide from New Guinea to Peru, and not much narrower in any latitude where cotton could thrive. Migration across a land bridge of this magnitude would not only take a vast amount of time, but would also presuppose very close ecological adaptation to the area if the migrating species were to obtain a foothold, let alone spread so widely in competition with other vegetation. To suppose that any species so well adapted and so aggressive as to cross a 10,000 mile land bridge by natural means, would leave no local races behind on any of the island relics of the bridge, is beyond reasonable belief. Yet from the longitude of Guam to that of the Revillo Gigedo Islands there is not a single record of the occurrence of a diploid cotton north of the continent of Australia, though the existence of ecologically suitable habitats is proven by the presence of the allopolyploids *G. hirsutum* var. *punctatum* in Polynesia and *G. tomentosum* in Hawaii. Even supposing the Pacific is not an ancient ocean, therefore, and land bridges across it existed from time to time, there is no reason to believe that diploid cottons ever crossed by them.

It will be seen that the genetic and cytological data justify the assumption of closer homology between the New World cottons and their nearest diploid relatives, and a more recent origin for allopolyploidy, than the proponents of the land bridge theory supposed. Firstly, all the allopolyploid species bear lint, and the only other lint-bearing species are the Old World cottons, carrying the A genom. Since the differentiation of the A genom has been shown to be bound up with the improvement of lint by civilized man, A-bearing, linted allopolyploids can only have arisen since the origin of human civilization. Secondly, on cytological, morphological, and phenogenetic behaviour, *G. raimondii* is more closely related to the New World cottons than any other species carrying the D genom. This also indicates a recent origin for the New World cottons, since it suggests that the American diploid species were differentiated *inter se* before the occurrence of allopolyploidy. Such a recent origin rules out any theory of natural spread to account for the meeting of the diploid parents, solely on the inadequacy of the time available. Only one alternative remains, that they were carried across the Pacific by man among the seeds of his crop plants and with the tools of his civilization. The absence of diploid cottons in the Pacific islands then becomes explicable. Close local adaptation is not essential in a cultivated plant. So long as the ground is cleared, the seed planted and the young crop weeded, a general suitability to the climate will suffice, but when the cultivation is abandoned, survival depends on successful competition with the local flora, and there is considerable evidence that among the cottons this can only occur in the special circumstances of open associations and limited competition. In the well watered areas that would attract the first colonists, once artificial clearing ceased, cotton would be choked in the regenerating forest. That the Old World cottons do in fact disappear completely when left to themselves in the New World is shown by the absence of records of their occurrence except under experimental culture. Watt (1907) records early introductions of Old World cottons into the United States, and specimens of *G. arboreum*, said to be spontaneous, were collected in British Guiana by Jenman in 1889 (Jenman's 5,149 in the Kew herbarium), but there is no record of their persistence, and all experience with Old World cottons at the Cotton Research Station supports the view that they would not survive longer than a year or two if abandoned.



In contrast, Upland cottons (*G. hirsutum*) although comparatively poorly adapted to Indian conditions, have persisted as admixtures in unselected crops of *G. arboreum* cottons in Central India for over a century (Hutchinson and Ghosé 1937a).

Since diploid cottons are absent from the Pacific, it is necessary to examine the history of cotton in the New World for evidence on which to test the theory that their Old World diploid parents were introduced by man. The cytogenetic evidence is clear that there is no reason to postulate more than a single origin for allopolyploidy. Chromosome differentiation among the allopolyploid species is very slight, and the species distinctions are due to the accumulation of gene differences. Two centres of variability are known, in southern Mexico and Guatemala for *G. hirsutum* and in the Andean valleys from Bolivia to Colombia for *G. barbadense*. The wild *G. tomentosum* is endemic in Hawaii. Practically every character found in the other allopolyploid species is to be found in *G. barbadense* in its area of high variability, whereas some characters known in *G. barbadense* are absent from the other species. The range of variation in lint characters is much greater in *G. barbadense* than in the other species, and in the area of high variability there is none of the morphological differentiation which accompanies specialization to particular climatic zones in the varieties of *G. hirsutum*. Instead, there is to be found a morphologically undifferentiated variability, such that the range of the species is from extremely arid conditions on the Peruvian coast to the moist tropical climate of the upper Amazon valley, without any marked separation into distinct types. The botanical evidence indicates, therefore, that the original home of the New World cottons was in the mountain valleys of north western South America. In this area *G. raimondii* is the only wild diploid species. Its cytological affinities with the allopolyploids, and its morphological suitability as a parent of New World cottons, have been discussed above. To that evidence may now be added the appropriateness of its geographical and ecological distribution. It is the wild cotton of the river valleys of Northern Peru, where, of all the Pacific coast line of America, the conditions are most favourable for the establishment of a new civilization by wanderers from the ancient cultures of the Old World. Here was water in the rivers, and fertile alluvium on the banks, and no great forests or other heavy vegetation to occupy the settlers

with the hard labour of clearing the land to the exclusion of the practice of the arts. And here, where they would plant their cultivated cotton on the banks of the streams, the appropriate wild species was indigenous. With a large population of the cultivated cotton as female parent, and a sufficiency of pollen from the naturally occurring wild species as male, the optimum conditions would be provided for the hybridization, without which allopolyploidy could not occur.

As with the cottons of the Old World, the distribution of the wild forms of the cultivated New World cottons is as would be expected, on the theory that their origin and development were intimately connected with their utilization by man. The areas of high variability of the cultivated species are the areas in which the ancient cotton-using civilizations of the New World flourished. The wild forms of these species are to be found more commonly near the peripheries of their areas of distribution than at their centres. They occur in open plant communities, such as dry coastal areas in the West Indian islands, and in many cases they occupy situations, such as secondary xerophytic scrub lands, that would never have come into existence but for the destruction of the closed forest for agricultural purposes, and wherever they are found they are closely related to the nearest cultivated forms. The inference that they are secondarily wild is supported by evidence that recently cultivated cottons have become established in natural vegetation. Forms of *G. hirsutum* var. *marie-galante*, relics of the perennial cotton cultivation of the eighteenth century, are to be found in all West Indian islands. Where the forest canopy regenerates rapidly in abandoned land they are confined to house yards and other artificial clearings. Where conditions are such as to retard forest regeneration, *marie-galante* cottons have become a natural component of the secondary open bush that develops. Evidence of more than one period of reversion to the wild is to be found in some islands, as for instance in Antigua, where a small-seeded, sparse-linted type is to be found in the older xerophytic scrub lands, while in the more mesophytic fringing forest along the creeks, a larger-seeded, better-linted form is found that is indistinguishable from the house-yard type descended from the cultivated cottons of the eighteenth century. Similar cases are known in *G. hirsutum* var. *punctatum* in its natural habitat on the coast of the Gulf of Mexico, and in many parts of the world to which it has been

introduced, and many instances could be cited from the perennial cottons of the Old World. Only the annual cottons have lost the capacity to re-establish themselves in wild vegetation.

The capacity of cultivated cottons to revert to the wild is of considerable interest and importance. Not only has the evolution of lint made possible a vast extension of the area occupied by species of *Gossypium*, but sufficient plasticity remains in the perennial forms, to permit of independent spread beyond the limits of cultivation into the type of open xerophytic vegetation to which *Gossypium* is peculiarly adapted. If it is accepted that the allopolyploid cottons arose under cultivation in the New World, it must be supposed that the wild *G. tomentosum* of arid plains in Hawaii is also a secondarily wild species. It bears true lint, and the chromosome pairing and genetic behaviour of hybrids between *G. tomentosum* and *G. barbadense* and *G. hirsutum*, indicate that it is not much more distantly related to them than they are to each other. In this respect it resembles the endemic Hawaiian species of other Neotropical genera, of which Skottsberg (1939) stated that, 'The species may be endemic but are seldom strongly marked, standing close to American species.' The means by which Hawaiian plants reached the islands have been the cause of much controversy, and it may at least provide an hypothesis worth testing against the species of the other genera of the Neotropical group to suggest that in view of its close relationship to the New World cottons, *G. tomentosum* can only have reached Hawaii since the establishment of civilization in tropical America.

The archaeological record also adds its quota to the evidence for the introduction of cotton to America by civilized man. In the desert graves of pre-Inca Peru have been found the spinning and weaving instruments with which cotton and various native wools were manufactured in the earliest known South American cultures. Of their spindles Crawford (1942) records that the same device was used in Peru as was employed by the fine spinners of the Dacca muslins in India. Of their looms he states (Crawford 1924) that the two-barred cotton loom is common to the cotton weaving areas of the Old and New Worlds, whereas the older warp weighted loom of the more northern flax and wool areas only occurs in the New World in coastal Alaska, where it is an obvious introduction from Asia by way of the Bering Straits. He concludes, 'The fact that this (two-

barred) type of loom originated in India and spread to Europe, that we find it together with the technical subtleties of fabric construction in the cotton areas of the New World, is difficult to explain except on the assumption of direct or indirect social contact.'

To conclude, it has been shown that in the area of greatest variability of the New World cultivated species is to be found their nearest relative among the American diploid species, but no wild linted type that could be regarded as ancestral to the cultivated races. In the same area an ancient civilization was located which used cotton as its basic textile and spun and wove it with instruments that differed in no essential particular from those used in Asia. Both biological and ethnological data, therefore, support the view that the allopolyploids originated under cultivation. The great strength of the theory lies in the fact that not only are the main biological and ethnological arguments independent, but the biological argument is itself composed of a series of independent lines of evidence. With so many separate inquiries yielding the same answer, there is scarcely room for doubt that the cottons of the New World as well as those of the Old owe their origin to the activities of civilized man.

## PART THREE

# *THE DIFFERENTIATION OF THE TRUE COTTONS*

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## I. INTRODUCTION

THE earliest civilization to spin and weave cotton was that of the Indus valley (see Part II), and for many centuries the cotton plant was known outside India only in travellers' tales. The fragments of cotton fabrics found at Mohenjo-Daro have been dated at approximately 3000 B.C. (Gulati and Turner, 1928). Yet though Mohenjo-Daro had contact with Babylonia, the textiles of Babylonia and Egypt were still of wool and linen when Herodotus wrote in 445 B.C. The north-eastward extension took place even later, cotton having been developed as a crop in China between the seventh and the thirteenth centuries of the present era. It is difficult to estimate the age of the crop in the New World as the Andean civilizations had no system of dating (Mangelsdorf and Reeves, 1939), but it does not appear to be usual to look much beyond the beginning of the Christian era for the establishment of the early cultures of the New World (Strong 1943)—a date approximately three thousand years after that ascribed to the Mohenjo-Daro fragments, which were themselves the products of mature craftsmanship. It is in the geographical and ecological conditions in the regions round the Indus valley, therefore, that the factors governing the primary differentiation of the cottons must be sought.

Early changes accompanying domestication, and the extent of the initial distribution of the new crop plant, must remain largely conjectural, but important modifications in response to the demands of comparatively recent large-scale agriculture can be traced with certainty in all cultivated species. Certain early changes were common to all. At first, purely agricultural qualities, such as large capsule and large seed with prompt germination to eliminate stand hazards, may have been favoured. Technical considerations, as distinct from agricultural, were also of prime importance. Although at first these must have primarily concerned the development of a copious, long, and

easily detachable lint, subsequent general aims have been less consistent, for they have been dependent at any particular time upon man's cultural or mechanical level of attainment. In the Indian cottons, for example, at the time of the fine Dacca muslins, fineness of lint was an important characteristic (Ahmad 1938). Later, the advent of power-ginning placed emphasis upon the ginning outturn of a cotton, and in response to the demand for a high proportion of lint to seed, types with coarser lint were selected (Hutchinson and Govande, 1938). A rather different type of differential selection within a single evolutionary line has recently been described in relation to lint colour, and its effect on the genotypic basis of the character has been discussed (Silow 1944a). Primitive cottons, like the wild species, no doubt had highly coloured lint. As man's artistic interests in design were aroused, the coloured and white extremes were favoured to permit pattern-weaving. More recently uniform white lint has been required to meet the demands of large-scale industry, but the genetic systems set up in response to the selection of the two extremes still persist.

As cotton cultivation extended, another agricultural factor became of increasing importance. Historical and botanical evidence are equally emphatic that the primitive cottons were perennial, but the bulk of the world's crop is now grown as an annual in areas where there is a long dry season or which are subject to frost, and even in areas where perennials can make satisfactory growth a demand has recently arisen for annual forms to facilitate pest control. The dimorphic branching habit of *Gossypium* made the development of early cottons primarily a matter of selecting types producing the first fruiting branch low down on the main stem. This was done with great success in the Old World species, leading to the establishment of the cotton crop in China, Northern India, Persia and Turkestan, (see Hutchinson 1938), and in those of the New World, giving rise to the Upland and Sea Island cottons in the United States. The development of annual types constitutes a fundamental change in the whole physiology of the plant, and has been as important a factor in the establishment of cotton as an economic crop as the improvement of capsule size and lint quality.

Fig. 7  
Distribution of  
G. ARBOREUM

Perennials —→  
Annuals - - ->

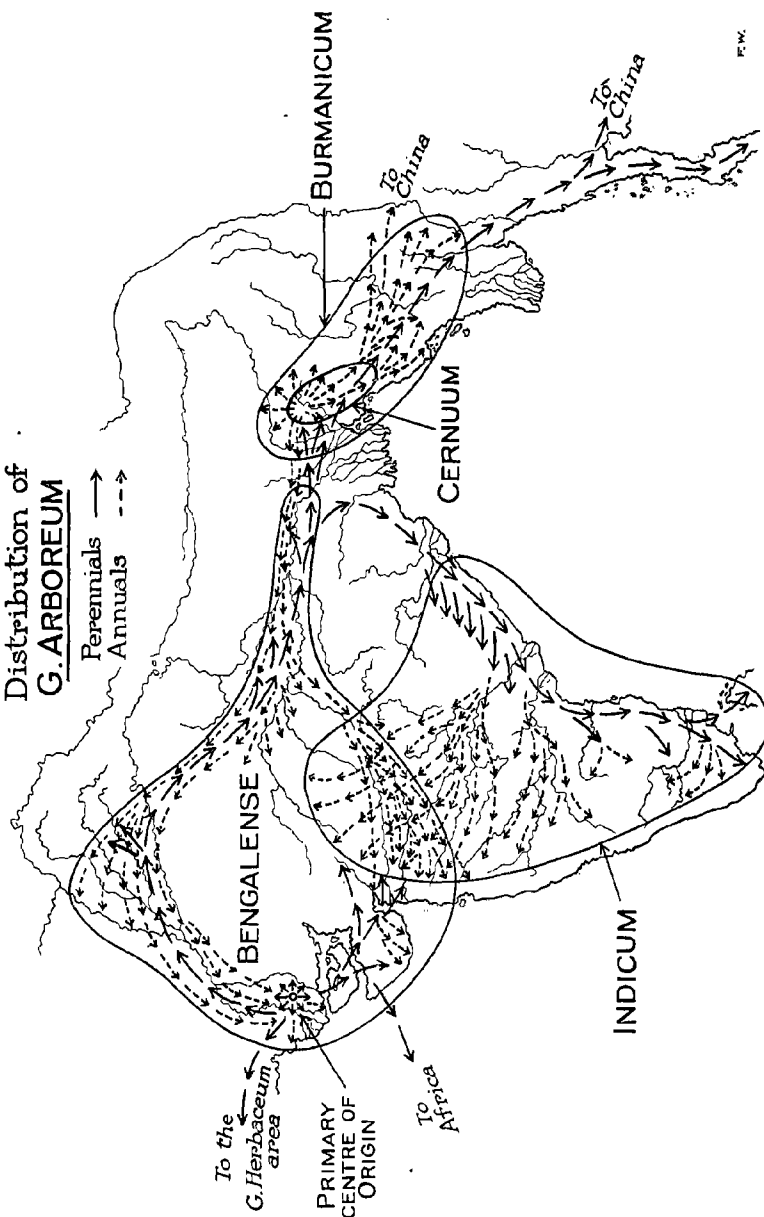


FIG. 7. Distribution of *G. arborescens*.

## II. THE COTTONS OF THE OLD WORLD

**D**IFFERENTIATION in the Old World complex of cultivated cottons has led to the establishment of two clearly defined species, *G. arboreum* and *G. herbaceum*. Each covers a very wide area, and accordingly exhibits considerable diversity. This situation led to much taxonomic confusion, which has been clarified only recently. In 1928, the Russian botanist Zaitzev (1928) first drew the broad distinction between *G. arboreum* in India and China, and *G. herbaceum* in Africa and the Levant countries. On the basis of subsequent comprehensive genotypic and taxonomic surveys in Trinidad and India, satisfactory subclassifications of these species have been formulated. In *G. arboreum* intra-specific differentiation is not great enough to justify the establishment of varietal distinctions, and the species is divided into six geographical races, *soudanense* in Africa, *indicum* in Peninsular India, *burmanicum* in East Bengal, Assam, and Burma, *cernuum* in East Bengal and Assam, *sinense* in China and *bengalense* in Northern and Central India (Silow 1944b). In *G. herbaceum*, intra-specific differentiation has progressed further, and three comparatively well-defined varieties are recognized; typical *G. herbaceum* in Central Asia and the Levant, *G. herbaceum* var. *acerifolium* in Western India and the Sudan area in Africa, and *G. herbaceum* var. *africanum* in South Africa and the Sudan (Hutchinson and Ghose, 1937b). The distributions of these varieties and races are mapped in Figs. 7 and 8. The evolutionary processes by which this taxonomic situation has arisen will now be discussed.

The distribution of the early cottons of India has been obscured by the spread in Northern India during the last century or so of the coarse stapled, early annual forms of *G. arboreum* race *bengalense*. Fortunately, there is good historical evidence of the types grown before the age of machine spinning, and their relics are to be found in sufficient numbers to make possible a reconstruction of their early distribution. In the thirteenth century all Indian cottons were perennials, and in parts of the



country perennial cultivation persisted until quite recent times. The accounts of Marco Polo, the Rev. E. Terry, and Mir Mohammed Masum have been summarized by Wait (1907), who concluded that in Western India and Sind the perennial Rozi form of *G. arboreum*, now confined to parts of Gujerat, was formerly the commercial type. Rozi is no longer found in Sind,

Fig. 8  
Distribution of  
*G. HERBACEUM*

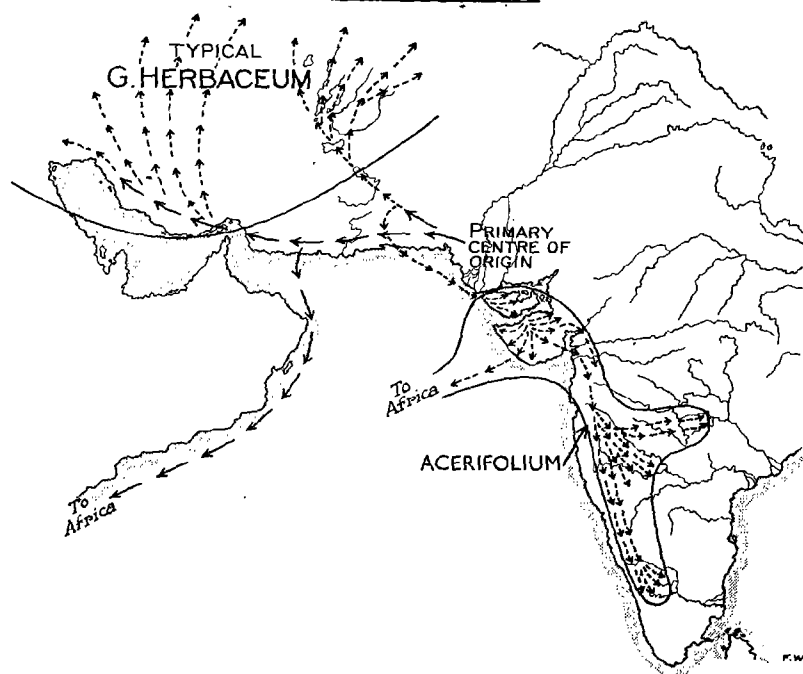


FIG. 8. Distribution of *G. herbaceum*.

but in both Sind and Rajputana, in villages beyond the limits of the great commercial cotton tracts, a late annual or semi-perennial, shrubby type of *G. arboreum* occurs, that is closely related to it. Farther east similar types are to be found, as, for example, the *G. intermedium* (Gammie 1907) of the United Provinces and the Podupathi (Ramanathan 1938) of the nor-

thern districts of the Madras Presidency around Vizagapatam. From a centre in Sind (see Part II) the spread of culture in an uncivilized country, either uninhabited or frequented by food-gathering tribes, would naturally be coastwise, and up the great river valleys. Accepting, then, the belief that cotton was the textile material of the earliest Indian civilization, its primary dispersion would be into Western India on the one hand, and the Punjab on the other. Conditions would not be favourable for any great extension from Western India. The valleys of the Nerbudda and the Tapti might be colonized, but extensive development would be limited by the lack of cereals. Wheat is near its southern limit in Khandesh. Rice was found and domesticated only on the coasts of the Bay of Bengal, and was therefore not acquired until the Indian Peninsula had been crossed, and it may be conjectured that *Sorghum durra*, which originated in Africa, did not reach India until a later date, possibly with the exchange of crop plants by which cotton reached Africa.

No such handicap would limit the spread of civilization up the river valleys of the Punjab. Wheat is grown successfully throughout the alluvial tract of Northern India until the rice area is reached, and it cannot be doubted that a vigorous, expanding civilization would take in the Punjab and spread through the Delhi gap into the valley of the Ganges. With the colonization of Bengal and the domestication of rice, the way was open for the growth of the rice-eating civilizations of the river valleys of the eastern coast. Cotton and rice, however, differ widely in their agricultural requirements, and with the establishment of rice as the staple food, there would arise an agricultural differentiation, rice occupying the irrigable flats and cotton being relegated to the higher and drier lands. On the eastern coast the distances involved are not great, and the cotton areas of the Madras Presidency are within easy reach of the rice-growing river deltas. In Bengal, however, the vast low-lying tracts of the Ganges and Brahmaputra deltas grow little cotton, and the textile crafts of the cities were supplied with raw cotton from the higher lands in East Bengal and Assam. Hence arose a partial geographical isolation that was to have important consequences in the differentiation of the *G. arboreum* cottons. In East Bengal and Assam there developed the centre of variability comprising race *burmanicum*, from which sprang

the races *cernuum*, *sinense* and *bengalense*, while in the Vizag district of northern Madras is to be found the variable material in which race *indicum* was differentiated.

The eastward spread of perennial types of *G. arboreum* did not cease at the boundaries of India. They are to be found in Burma and Indo-China, Malaya, the Dutch East Indies and the Philippines, as far east as Timor Laut and Guam, and are recorded as having reached China about the seventh century of the present era. It is among these, the least specialized of the forms of *G. arboreum*, that reversion to the wild is frequently found. Watt (1907) has described the wild and cultivated forms of Rozi in Gujerat, where the upright cultivated type with large bolls, large seeds, and good and copious lint has as its counterpart the sub-scandent wild form of hedgerows and waste places, with small bolls and seeds, and poor and scanty lint. Their close relationship is so obvious that Watt (1907) and others have had no hesitation in describing the latter as recent escapes from cultivation. In the east, where perennial cottons are no longer cultivated, or where, as in the East Indies, cotton has given place entirely to other crops, there are not such obvious examples of the parallelism between wild and cultivated forms, but the status of the feral types as escapes is established by historical evidence of cultivation, and by the use of the Indian name (kapas; Sanskrit Karpasa) to describe them in Java, Macassar, and the Philippines (Watt 1907).

The origin of the cottons found west of the Indus valley must now be considered. It has been suggested (Hutchinson 1938) that the cultivated cottons of the species *G. herbaceum* were derived by selection from the perennial wild *G. herbaceum* var. *africanum* of the South African bushveld, and that the species spread in Asia following the introduction of agricultural types from Africa. Such an hypothesis is tenable only so long as it is believed that the differentiation of the two species antedated the adoption of cotton as a textile by man, and is inconsistent with the theory put forward above that the development of the linted cottons proceeded *pari passu* with their exploitation as a crop plant. Moreover, it offers no satisfactory explanation of the fact that *G. arboreum* occurs in all the areas in Africa from which *G. herbaceum* has been recorded, and in some from which the latter is absent. Since ancient records all point to Sind as the original centre of cultivation of cotton, the possibility that

*G. herbaceum* arose by differentiation in a westward diffusion of the Sind crop may be considered.

According to Watt (1907) and Massey (1924) the first account of cotton outside the western boundaries of India was given in 350 B.C. by Theophrastus, who described the 'wool-bearing trees' of Tylos (Bahrein, in the Persian Gulf), and stated that cotton was cultivated in Arabia as well as India. How long perennial cottons had been established there is a matter for conjecture, but since there is known to have been contact between Mohenjo-Daro and contemporary civilizations in Babylonia, it seems likely that the cottons of the Indus valley were distributed along the Persian coast and as far up the Persian Gulf as perennials could be successfully grown. The collapse of the Indus civilization in the middle of the third millennium B.C. (Childe 1942) effectually divided the cotton area in two, since in the absence of a well-organized community to maintain irrigation facilities, Sind and Rajputana present a practically complete desert barrier between Persia and Peninsular India. In the isolation so established may be found the conditions under which genetic divergence took place and led to the establishment of the species distinction between *G. herbaceum* and *G. arboreum*.

Here ends the first phase of the evolution of the cottons. To this point the dominant factors influencing the success of the crop were those governing adaptability to the conditions of the natural environment, together with the seed cotton and lint characters conducive to satisfactory yield and good spinning behaviour. With increasing population, the spread of agriculture to less favourable land, and the establishment of more exacting standards of civilization, the conditions for success changed, and a radical alteration in selective forces came about.

By far the greatest change consequent on the intensification of agriculture was the establishment of the supremacy of the annual cottons. As has been pointed out above, the dimorphic branching habit of *Gossypium* renders it peculiarly susceptible to change in the length of the vegetative period. Annual cottons have, in fact, repeatedly been developed by local selection, and only in exceptional cases have perennials been replaced by annuals introduced from elsewhere. In Persia the spread of the cotton crop must have been very sharply limited by the severity of the winter season until annual cottons were selected, and in

consequence the establishment of the annual habit was achieved earlier in *G. herbaceum* than in *G. arboreum*. Ramanathan (1938), who first put forward the view that the var. *acerifolium* cottons had been brought to India from the north, quoted Marco Polo's statement that annual cottons were known in Yarkand in the thirteenth century, when the Gujerat cottons were trees 20–30 feet high. Ansari (1940), commenting on the importance of earliness in Iran, stated that, 'The *herbaceums* that were come across were all highly sympodial as would be expected in a country with early frosts and severe winters. To hasten maturity, it is a general practice in Iran to pluck the leaves and top the plants at all stages from the bud to the boll-forming period.' Evidently, selection for the annual habit must have been strong from early times, and the effect of this selection is shown in the predominance of small, early forms in the north of the country (Ansari 1940). Within the limits of the one variety there is every gradation between the perennials of Mekran (Ansari 1941) and the short season annuals of Chinese Turkestan, among which are the earliest fruiting cottons known. With the establishment of the annual types now classified as typical *G. herbaceum* in Persia, Afghanistan, and Turkestan a new centre of variability arose, in which a considerable range of morphological and technological characters is to be found (Chernyakovskaya, 1930; Bordakov and Ivanova, 1935; Ansari 1940).

In Western India no perennial forms of *G. herbaceum* are known. The species is represented by var. *acerifolium*, which is an annual, but which still carries an important character usually associated with the perennial habit. So long as wet weather continues, all flower buds are shed at a very early stage. This type of bud-shedding, which Mason has termed 'facultative shedding' (Harland 1939), serves in perennials to time the onset of the crop correctly. In var. *acerifolium* also, it ensures that fruiting occurs in dry weather, but since an annual plant fruits only once, the facultative shedding mechanism is no longer essential, and in most annual cottons the fruiting branches appear at the right time to ensure cropping in the dry season.

Although var. *acerifolium* has not been reported from Mekran or Persia, Ansari (1940) has recorded the occurrence of intermediates among the typical *G. herbaceum* cottons of Persia, and the Wagad types of Kathiawar and Cutch have the practically indehiscent capsule characteristic of many forms of typical

*G. herbaceum*. These form a connecting link between the Persian and Western Indian types. Trade between the ports of Western India and Mekran and Persia has gone on for many centuries, and it would therefore be natural for seed exchange to take place between the two areas. Hence, it is likely that the value of the annual habit in Western India was demonstrated by the success of crops grown from Persian seed, and the var. *acerifolium* cottons developed subsequently with the spread of the introduced type. On the whole they form a comparatively uniform assemblage, with a centre of variability in Gujerat (Hutchinson 1938). Here there is considerable variability in bushiness, earliness and quality. In northern Kathiawar and Cutch the Wagad form predominates. To the south of Gujerat, through the Decan, a progressive increase in earliness may be observed (Hutchinson and Ghose, 1937b), culminating in the Uppams of the Madras Presidency, in which the facultative shedding habit appears to have been lost.

It will be convenient to survey the distribution of the Old World cottons in Africa before discussing the development of the annual forms of *G. arboreum*, since practically all the *G. arboreum* cottons in Africa are perennial. The circumstances under which cotton reached Africa are unknown, but there is good evidence that it was not known in Egypt before about the fifth century B.C. In the time of the Kingdom of Meroë, about 500 B.C. to A.D. 300, cotton had become established in the Sudan region, and it has been suggested (Griffith and Crowfoot, 1934) that the cotton trade was one of the sources of Meroitic wealth. From the Sudan, cotton doubtless spread across the savannah country between the Sahara and the Central and West African forests, providing raw material for textile crafts among the indigenous peoples, that persist to this day. Cottons were also introduced along the east coast of Africa, and spread south as far as Delagoa Bay, and across southern Africa to Angola. The spinning and weaving of cotton never seems to have had such an important place in South Africa as in the north, but De Barros (c. 1560) said of the Monomotapa (ruler of Zimbabwe) that 'the greatest ornaments of his house are cotton cloths made in the country with much labour' (Kenyon 1931).

In all these areas *G. arboreum* and *G. herbaceum* are found together at the present time, except in the coastal belt of Kenya and Tanganyika, where only *G. arboreum* has been found. All,

or nearly all the *G. arboreum* types are perennial, and among them are forms so like those of India as to have been labelled Rozi by Watt. Chevalier (1936) has applied var. *neglectum* to forms of *G. arboreum* from French West Africa and the French Sudan, but from an examination of specimens in the Kew herbarium, and from such notes on growth habit as can be discovered, it seems unlikely that they have the annual habit which Hutchinson and Ghose regarded as characteristic of the variety. Chevalier states that the *G. arboreum* type is no longer grown for its lint, but as a fetish, or as a medicinal plant.

The African forms of *G. herbaceum* belong to two varieties, var. *africanum*, which is perennial and is now found only as a wild plant, and var. *acerifolium*, which is recorded from the savannah countries of the Sudan tract, and according to Chevalier (1936) was the cultivated type before the introduction of New World cottons, and persists in relic cultivations among many tribes. Specimens of var. *acerifolium* were collected by Sir John Kirk in 1860 from native cultivations in Nyasaland and Zambesia, but the type now appears to have vanished entirely from southern Africa (H. C. Ducker, in correspondence). In the Sudan area Chevalier (1936) states that intermediate types between var. *acerifolium* and var. *africanum* occur spontaneously in fallows and abandoned cultivations, but are not truly wild. Specimens indistinguishable from true var. *africanum* have been collected in Nubia and Libya. In the bushveld areas of South Africa and Southern Rhodesia, var. *africanum* is the native wild cotton.

The coastal trade route linking up Western India, the Persian Gulf, the Red Sea, and the East African coast has been in regular use for so long that it can scarcely be doubted that cottons from India and Persia have been introduced many times into Africa. It is therefore possible to reconstruct the history of the cottons of Africa only from botanical evidence, and from such data as are available on the course of the cotton trade. Since the cottons of India and Bahrein were perennials in the fourth century B.C., it may be accepted that the first African types, on which the Meroitic trade was based, were also perennial. There seems no reason to doubt that *G. herbaceum* and *G. arboreum* were both introduced at an early date, since their perennial representatives in Africa are of what must be regarded as primitive types. Types of *G. herbaceum* var. *acerifolium* have been collected in West Africa, that are morphologically indis-

tinguishable from those of Western India, and the conclusion is unavoidable that they represent introductions from Western India or from the immediate progenitors of the Western Indian types in Persia. The occurrence of intermediate types in West Africa is in conformity with the status of the crop in other parts of the world where two varieties of the same species have come together and a variable hybrid population has arisen.

The history of the Old World cottons in Africa, then, was probably as follows:

Perennials of the Rozi type in *G. arboreum* and a progenitor of *G. herbaceum* var. *africanum*, possibly the Tylos cotton of Theophrastus, were early introduced into Africa, and gave rise to the first African cotton trade in the Kingdom of Meroë. They spread wherever there were people capable of spinning cotton, and were supplemented by later introductions, notably of *G. herbaceum* var. *acerifolium*. The latter, being a better cotton, and being capable of cultivation as an annual, became the main cultivated type, until the arrival of the cottons of the New World. The older perennials were abandoned except where they were grown for magical or medicinal purposes, but became established as wild plants in the natural vegetation. Hybridization between the cultivated var. *acerifolium* and the secondarily wild var. *africanum* in West Africa has resulted in the development of an intermediate type which occurs as a colonist in secondary vegetation.

With the advent of New World cottons, var. *acerifolium* was also displaced, but being predominantly annual in habit, has not become established in the wild. It has vanished from the southern area, and is likely to disappear from the Sudan region in due course.

In the long run, the extinction of connecting types by the divergent selective forces operating in the three areas occupied by *G. herbaceum* will lead to the isolation of the type and the two varieties in Central Asia, India, and Africa respectively. The establishment of a distinct *soudanense* type of *G. arboreum* is also in progress, but while perennial forms persist in Asia, it will not be so widely separated from the rest of the species as *G. herbaceum* var. *africanum* will be from the type and var. *acerifolium*.

The development of annual types in *G. arboreum* will now be considered. According to Ramanathan (1938), in race *indicum* broad-leaved perennials spread south along the Indian coast



as far as Tinnivelly, and the modern Podupathi of the Vizag district and the Nadam of Tinnivelly are morphologically indistinguishable. Inland from the Coconadas tract, however, the need for cottons suited to the Deccan, with its hot dry summers, led to the evolution of the annual Bani, which spread through northern Hyderabad, Berar, Nimar, and Khandesh, and gave rise to the old fine 'Oomras' of the eighteenth century.

In the south, Ramanathan (1938) states that the annual Karunganni was developed only about a century ago from the perennials of Tinnivelly. Since then, annuals have been favoured on account of the advantages they offer for the control of pests, and the only perennial cotton now remaining in South India is the small Nadam crop.

The strongest selective force encountered by these cottons was human selection for fine quality. Ahmad (1938) states that the Dacca muslins were made from cotton with a staple of about an inch, and a hair weight of  $0.12-0.15 \times 10^{-6}$  oz. per inch—a standard of quality unequalled by any indigenous cotton among the Standard Indian Cottons of the present day (Ahmad 1942), and approached only by some of the *G. arboreum* race *indicum* cottons of Peninsular India and the best of the *G. herbaceum* var. *acerifolium* types. Though the Dacca muslins are the best known of India's fine textiles, fine spinning and weaving was carried on in all parts of India, and fine cottons, some of which were exported to Dacca (Royle, quoted by Hutchinson and Ghose, 1937a) were grown to meet the demand.

These cottons were the cottons of old Hindu India. To meet the demands of her wealthy rulers, India developed a craftsmanship that has never been matched, and fine cottons that can to-day be excelled only in the New World species. Agriculturally, however, the types changed only slowly from the perennial ancestral form, and in consequence it is to the *indicum* cottons that *G. herbaceum* is most closely allied (Silow 1944b).

Meanwhile, in eastern Bengal, Assam, and Burma, the northern Indian type was undergoing extensive differentiation, and a major centre of variability arose (race *burmanicum* of Silow 1944b). Here are to be found many perennials, various types of intermediate duration, and a high proportion of annuals. In quality characters, all degrees are met with. The upper quality limit was the fine cotton of East Bengal that provided the bulk of the raw material for the Dacca muslin industry (Price,

quoted by Hutchinson 1938), while at the other end of the scale are the short and extremely coarse types which are sold with race *cernuum* in the Comillas crop.

From this major centre of variability there have been three independent developments of annual types. One of them is of comparatively minor local importance. This is the big-bolled *cernuum* group of the Assam hills, to which Hutchinson and Ghose (1937b) gave varietal status on account of its distinctive morphological features. It is really only an ecotype representing the end-product of localized selection tendencies, and has been retained as a distinct geographic race only on account of the established agricultural usage of the name. The other two territorial extensions of annual types are of great importance. The older one was into China, Japan, Manchuria, and Formosa. No perennials remain in this area, but there are historical records that such forms were introduced into China as garden plants in the seventh century. By the thirteenth century a commercial crop had been established, based on extremely early-fruited types developed from Indian and Indo-Chinese introductions. Within the limits of the early habit imposed by the short growing season, such a wide range of variation has developed that race *sinense* now constitutes a new and extremely important centre of variability which may well lead to the eventual establishment of a full varietal distinction within *G. arboreum* (Silow 1944b).

By contrast, the remaining annual race, *bengalense*, comprises a rather uniform group of early, high-ginning, relatively coarse cottons which constitute the coarse Bengals and Oomras of the modern Indian cotton crop. As so defined, *bengalense* is one of the most recent races of *arboreum*, having spread during the last century from the hilly tracts of Eastern Bengal and Assam in response to the demand of the cotton industry for high ginning percentage with little regard for quality. The *bengalense* cottons proved the most profitable for the extension of cotton growing that took place in the United Provinces, in the developing canal colonies in the Punjab, and later in Sind (the 'Bengals' tract of commerce). Here they would meet the relics of the ancient cultures, the old *desi* cottons of Sind and Rajputana. Ramanaathan (1938) has shown that in certain anatomical features the *sanguineum* types of *G. arboreum* from the Punjab resemble the cottons of Peninsular India, while it is worthy of note that

the red leaf and flower gene of the *sanguineums* is common among the annual cottons of the Punjab and Sind, and has been recorded in perennial types of *G. arboreum* from Africa, Malaya, Java, and Macassar. The cotton of Mohenjo-Daro had a hair weight similar to that of the modern coarse *desi* cottons of the Punjab and Sind (Gulati and Turner, 1928) and vastly different from the fine types that reached their zenith in the days of the fine Indian muslins. There is therefore some reason to believe that the ancient north western Indian types have contributed to the annual *G. arboreum* race *bengalense* in the 'Bengals' tract.

In the 'Oomras' tract of the Central Provinces and the northern Deccan, *bengalense* types have been widely extended at the expense of finer *indicums* and in parts of Western India they have displaced *herbaceum* cottons. Though the premium for better quality is still outweighed by the extra return from quite a small increase in ginning percentage (Panse 1941), the extension of the area of the coarse *bengalense* cottons appears to have been arrested, partly by ecological factors (Hutchinson and Ghose, 1937a) and partly by recent administrative action taken to prevent the adulteration of the better *indicum* types.

In the northern part of the Deccan the three chief races of Indian cotton meet. From the north-west came *G. herbaceum* var. *acerifolium*, from the east, *G. arboreum* race *indicum*, and from the north-east, *G. arboreum* race *bengalense*. The resulting welter has been admirably studied by Sawhney (c. 1938) in a survey of the cottons of the Hyderabad State. *G. herbaceum* var. *acerifolium* is separated from the races of *G. arboreum* by a genetic barrier that is practically complete, and by ecological adaptabilities that result in its being confined almost entirely to the drier and cooler *rabi* season, while races of *G. arboreum* are more generally grown in the wetter, warmer *kharif* (monsoon) season. The barriers separating the races of *G. arboreum* are much less complete, and there is good evidence for the belief that the range of segregation products to be expected when hybridization occurs between geographical races of a single species, is to be found in the modern 'Oomras' crop of Hyderabad and the Central Provinces.

Cytological studies have revealed no differences in the gross structural arrangement of the chromosomes between the two species of Old World cottons, and Silow (1944b) has shown that the whole of the observed diversity, both inter- and intra-specific,

can be referred to the effects of manifold gene substitutions. In *G. arboreum* the old perennial types were distributed over a great area, but were subject to generally similar climatic conditions in almost all parts of it. The most important differential selection encountered was that for quality, so that though the modern representatives of the perennial stocks are morphologically comparatively uniform, there are to be found among them great differences in lint characters.

Divergent selection trends leading to morphological differentiation within the species became important only with the demand for annual cottons in extremely recent times, and while a very definite separation is developing between the race *sinense* and the Indian and Burmese cottons, no such clear division exists, or is likely to develop, between the races of the Indo-Burmese group. It may be said, in fact, that with the spread of race *bengalense* into the race *indicum* area, further divergence ceased, and from the success of such types as Verum and Jarila, which combine the characters of both, it may be concluded that fusion is in progress where their distributions overlap. So the low level of differentiation of the intra-specific groupings in *G. arboreum* may be ascribed to the late establishment of divergent selection trends, and the incomplete, and sometimes transient, geographical isolation between them.

Reasons have been given above for believing that the annual habit was established earlier in *G. herbaceum* than in *G. arboreum*, and that already established annuals of *G. herbaceum* var. *acerifolium* were introduced into Western India about the time when selection for the annual habit began in *G. arboreum*. Since that time, the three *G. herbaceum* areas have been geographically isolated, and the selection trends in them have been widely divergent. It is therefore not unexpected that intra-specific differentiation has reached varietal rank, and is well on the way to the establishment of a condition in which all intermediate types have vanished.

The analysis of the origin and present status of the varieties of *G. herbaceum* provides the key to the solution of the problem of the separation of *G. herbaceum* from *G. arboreum*. The level of intra-specific differentiation in *G. herbaceum* is higher than in *G. arboreum* because divergent selection trends have been operating for a longer time in better isolated groups. But for the existence of intermediate forms, there would be good reason

to regard the early annuals of *G. herbaceum* from Chinese Turkestan as specifically distinct from the perennial shrubs of *G. herbaceum* var. *africanum* from South Africa. The recombination products arising in their hybrids from the break-up of the co-ordinated gene systems governing habit alone would be sufficient to demonstrate the distinctness of the genetic balance of the two types. It is but a step from this degree of difference to that between the two species, between which divergent selection has been in operation much longer, and isolation, in the period following the collapse of the Indus civilization, was equally complete.

### III. THE COTTONS OF THE NEW WORLD

FROM the distribution of the Old World Cottons it will be seen that the only linted diploid species that could have been carried across the Pacific to western South America is *G. arboreum*, or a species ancestral to it. There is no evidence that *G. herbaceum* ever reached the Pacific and the present eastern limit of the distribution of *G. arboreum* coincides apparently with the limit of the area in which it has recently been used. It is recorded as an introduced ornamental shrub in Guam (Safford, quoted by Watt, 1907), but in the East Indies it was formerly cultivated in the Philippines, Java, and Macassar (see Watt, 1907). From the ecology of the species, it is not unexpected that it is not now to be found farther east. It is predominantly mesophytic in behaviour, and except where the climax vegetation is destroyed by man, mesophytic conditions in New Guinea and Polynesia lead to the development of closed forest associations in which *G. arboreum* would not survive. In conformity with this view, with two exceptions, records of New World cottons now established in that area all refer to types that are cultivated by man, or grown in association with him in house yards or cultivated clearings. The exceptions are the extremely xerophytic ecotype of *G. hirsutum* var. *punctatum*, formerly known as *G. taitense*, and *G. tomentosum*, both of which tolerate arid conditions where the climax vegetation is sufficiently open to permit the establishment of *Gossypium* seedlings.

The New World cottons are differentiated into three species between which genetic isolation barriers exist. *G. barbadense* is the South American cotton, and *G. hirsutum* has its centre of variability in Southern Mexico and Guatemala. The third species, *G. tomentosum*, is endemic in the Hawaiian islands. The three inter-cross freely, giving fully fertile  $F_1$  hybrids which exhibit considerable hybrid vigour. Skovsted (1937) has examined meiosis in the  $F_1$ s and found it normal. In  $F_2$ , however, extensive genetic breakdown occurs, giving rise to unbalanced types of low viability. Harland (1936a) has discussed the nature

of this species differentiation and has concluded that there is no evidence that any process besides gene substitution has been involved.

In  $F_2$  and later generations of *G. hirsutum* x *G. barbadense*, good germination and seedling establishment is obtainable, the unthrifty nature of many segregates becoming evident only as the plants develop. Nevertheless, the barrier is very effective, as is shown by the behaviour of mixtures of *G. barbadense* and *G. hirsutum* var. *marie-galante*, such as are to be found in the Marie-galante crop of the Grenadines, where the integrity of the species is maintained unimpaired in spite of the ease with which crossing occurs. Stephens (1946) has shown that in the areas where the two species have come together, the barrier to crossing is in process of becoming complete by the spread of the complementary corky mechanism through the forms occupying the area of overlap.

In crosses involving *G. tomentosum*, heavy losses in the seedling stage are the rule, and the raising of large progenies in  $F_2$  and later selfed generations is frequently a matter of considerable difficulty. In an  $F_2$  of *G. hirsutum* var. *punctatum* x *G. tomentosum* germination and seedling development were as follows:

Seeds with small embryos that failed to germinate	7
Seeds with apparently normal embryos that failed to germinate	36
Seedlings that failed to expand the cotyledons	9
Seedlings that died within three weeks	22
Unthrifty seedlings at three weeks old	16
Strong seedlings at three weeks old	20
	---
Total seeds sown	110

The genetic breakdown in the *G. tomentosum* cross began much earlier, and was much more serious, than it is in *G. hirsutum* x *G. barbadense*, and it must be concluded that *G. tomentosum* is genetically further removed from *G. hirsutum* than *G. hirsutum* is from *G. barbadense*. Comparable data are not available from *G. barbadense* x *G. tomentosum*, but Harland (1939) considered *G. tomentosum* to be nearer to *G. barbadense* than to *G. hirsutum*, and it is possible that breakdown in that hybrid might not be so serious as in the *G. hirsutum* cross.

Intra-specific differentiation has followed the same pattern as in the Old World cottons. In the area of distribution of *G. barbadense* in continental South America, there are no geographical

barriers to free interchange. In *G. hirsutum*, where distribution round the coasts of the Caribbean and the Gulf of Mexico has resulted in the establishment of a considerable degree of isolation between *G. hirsutum* and its vars. *marie-galante* and *punctatum*,

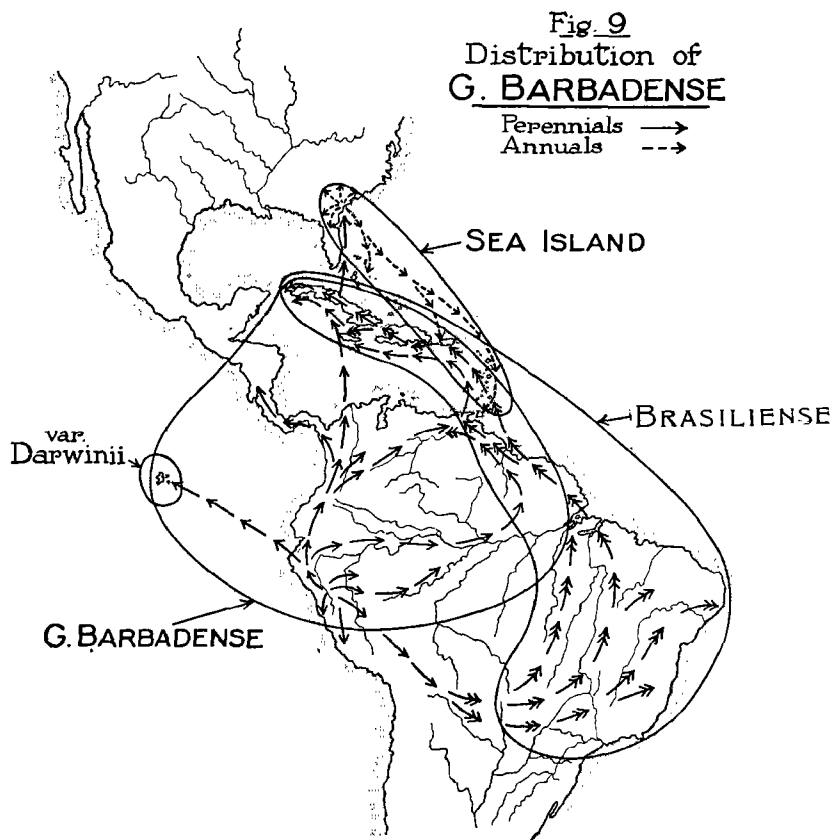


FIG. 9. Distribution of *G. barbadense*.

the distinctions have become so well marked that Harland (1939) has given them specific rank.

Since the differentiation of the species is the result of the accumulation of gene substitutions, it must have taken place in isolation. The isolation of *G. tomentosum* is complete and the only problem the species offers is that which it shares with the



rest of the Hawaiian flora of how it arrived there in the first place. The distributions of *G. barbadense* and *G. hirsutum* var. *marie-galante*, however, have overlapped since pre-Columbian times, and though they have different ecological optima, they are frequently found growing side by side. The centres of variability of the two species are widely separated, and are in the regions occupied by the ancient South and Central American civilizations. Evidence has already been presented for the view that the New World cottons arose in western South America, and Mangelsdorf and Reeves (1939), discussing the origin and distribution of maize, have shown that crop plants from the South American lowlands were taken to Central America, but that there was subsequently little or no agricultural exchange between the two areas. The evidence is therefore in accord with the view that an early introduction of cotton from South into Central America was followed by a period of isolation, during which the two crops were developed independently. It must be assumed that the spread to the east which resulted in the divergence of *G. hirsutum* var. *marie-galante* did not occur until the genetic differentiation of the species was well advanced.

*G. barbadense* is the cotton of the region of South America in which the allopolyploid species probably originated. Its distribution in the Americas is mapped in Fig. 9. Recently Mauer (1930) on the basis of Bukasov's collections, and Harland (1936b), judging by the extraordinary variability he observed in the Cauca valley, placed the centre of variability west of the Central Cordillera in Colombia, but recent additions to the C.R.S. collection give evidence of very high variability in cultivated, semi-cultivated, and spontaneous cottons throughout western South America as far south as Bolivia. Acquisitions from Piura, north Peru, have been contributed by the Agricultural Experiment Station of La Molina, Peru, and from the slopes and valleys of the Andes in Ecuador, Peru, and Bolivia, by E. K. Balls. In this collection is to be found great variability in habit, from long-lived perennials to late annuals, in the photoperiodic control of fruiting, in the degree of plant hairiness, and in boll size, surface pitting, shape and loculi number, together with all grades of quality from that of fine Egyptian to typical Rough Peruvian, and all shades of colour from deep mahogany red to light cream and pure white. From Balls's field notes it is evident that most of the South American cottons

are commensal with man, rather than systematically cultivated. They are rarely sown as a crop, but their produce is regularly collected and used for homespun textiles, and the plants that spring up from discarded seed are generally encouraged. In Tumbes in North Peru is found a wild type (Boza 1941) with scant and irregular lint, and in the Galapagos Islands there are spontaneous cottons of both typical *G. barbadense* and the endemic *G. barbadense* var. *darwinii*. An examination of material in the Gray herbarium showed that even in the Galapagos there is now no sharp varietal distinction. *G. barbadense* var. *darwinii* has certain distinct genetic characteristics and may represent an earlier differentiation from *G. barbadense* proper. The possibility must be borne in mind that the intergrading series now observed may be the result of hybridization between var. *darwinii*, the product of an early isolation, and more recently introduced forms of typical *G. barbadense*. The situation in the *G. barbadense* area is closely parallel to that in other cotton growing areas, where cultivated perennial types have escaped and become established as spontaneous components of natural vegetation. The intermediate stage, however, is more important than in Asia, and cottons which spring up around human habitations are regularly used, though they are not systematically cultivated.

*G. barbadense* is always grown as a perennial in the area of high variability in western South America. The cultivations of the Incas have given place to the commensal cottons of the Indian tribes and from these a commercial crop has been re-established in the coastal valleys of Peru. The dominant variety, Tanguis, is a perennial, wilt resistant selection, but it is of interest to note that the modern trend in favour of annual cottons for more intensive cultivation and better pest control is beginning to influence breeding policy (Boza 1940).

*G. barbadense* var. *brasiliense* appears to have been developed in response to the requirements of the peoples of the moist tropical forests of Brazil. In the area of high variability, the kidney character is found only in the south and then only rarely. It is not uncommon among the old established perennial cottons of the Argentine, and it may be suggested that its distribution into Brazil was from the south. At the present time, coarse linted forms of typical *G. barbadense* and var. *brasiliense* are common in the moister parts of north eastern South America

and have spread through the Lesser and Greater Antilles. The distribution of these and other perennial New World cottons in the West Indies in the eighteenth century, when perennial cotton was an important crop, has been discussed by Stephens (1944b) and Hutchinson and Stephens (1944). Hutchinson and Manning (1945) have given reasons for believing that finer *G. barbadense* types from western South America were also introduced into the Greater Antilles, whence the foundation stock of the fine Sea Island cottons was obtained in the 1780s.

The establishment of the Sea Island cottons in South Carolina in the latter part of the eighteenth century marks the beginning of the modern commercial types of *G. barbadense*. The annual habit was perforce established immediately, since all strains that did not fruit before winter were eliminated by frost, and it is evidence of the great variability existing in the perennial *G. barbadense* cottons of the time, that it was possible to select early cropping plants in the original introductions. The agricultural advantages of the annual habit of the Sea Island cottons have made possible the establishment of a stable cotton-growing industry in the West Indian islands, in the face of pests that rapidly reach epidemic proportions on perennial types. Owing to their specialization to meet a small demand for extreme length and fineness, they have not spread widely, and their most important contribution to the world's cottons has been the production, from Sea Island x perennial *G. barbadense* hybrids (Balls 1919), of the fine cottons that now constitute the Egyptian crop. In response to the environment of the Nile valley, a definite Egyptian type has been evolved, so that the Sea Islands and Egyptians must now be regarded as geographically and ecologically distinct.

Elsewhere in the Old World, *G. barbadense* has had little success, though it has been introduced and persists sporadically, generally as a commensal cotton, in many parts of Africa, Asia, and the islands of the Pacific. A small crop has been established in Southern Nigeria, based on selections from acclimatized types found growing as perennials in the Ishan district. Ishan is grown commercially as a late annual and fills a useful, though small, place in the agricultural system. It is of some importance as representing the coarser quality types of *G. barbadense* that are not at present very widely used.

The distribution of *G. hirsutum* in the Americas is mapped in

Fig. 10. Mauer (1930) has described the range of types to be found at the centre of variability of *G. hirsutum* in southern Mexico and Guatemala. He has recorded all types of habit, from annuals resembling Upland to medium-bolled, commensal perennial shrubs and small trees, and the small-bolled, wild shrub described by Watt as *G. palmerii*. The photoperiodic habit, characteristic of the tropical cottons, occurs in sympodial, potentially annual types as well as among the monopodial, highly vegetative perennials (*vide* Mauer, from experimental studies in Russia). Lint quality is very variable, and white, brown, and rust coloured lint occur, and were used, as in Peru and in the Old World, for weaving patterned cloth.

*G. hirsutum* has been distributed into three geographically and ecologically distinct areas, and morphologically distinct varieties have arisen. These are typical *G. hirsutum* (Upland), and the two varieties *punctatum* and *marie-galante*. The three varieties are distinguished primarily on their fruiting habit. All cottons naturally produce their crop in the dry season, but the proper timing of the onset of the reproductive phase is determined by widely different physiological mechanisms. In the annual Upland cottons the life history is short, so that a seedling established early in the wet season reaches the flowering stage as the rains abate, and completes its life before the end of the dry season. In the perennials, on the other hand, a periodicity is established so that successive crops are produced in the proper seasons of the year. Facultative shedding occurs in var. *punctatum*, all flower buds produced during wet weather being shed at a very early stage, so that although fruiting branches may be formed at any time, flowering is postponed until dry weather sets in. In var. *marie-galante* the primary factor in the control of fruiting is the photoperiodic habit. All growth is vegetative during the period of long days, which coincides with the wet season in the Caribbean region, and fruiting branches do not usually develop until the days shorten. Many *marie-galante* types are also facultative shedders, but since shedding can occur only after fruiting branches have been formed, it is in them an entirely secondary mechanism.

From the undifferentiated variability of the centre of origin in southern Mexico and Guatemala, distribution along the comparatively dry coastal belt of the Spanish Main led to the isolation of var. *marie-galante*, the largest of the cottons. This

Fig. 10  
Distribution of  
G. HIRSUTUM

Perennials —→  
Annuals ---→

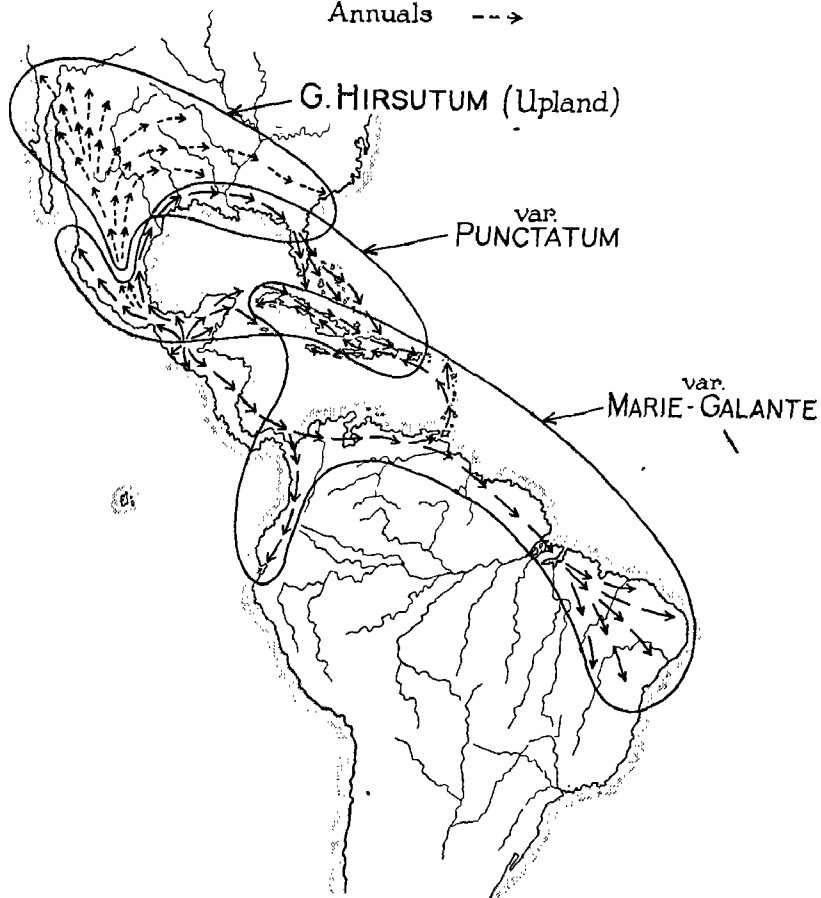


FIG. 10. Distribution of *G. hirsutum*.

F.W.

variety is a large shrub or small tree, up to 20 feet high. It has a wide range of ecological tolerance, occurring as a commensal in house yards and domestic clearings in areas with a rainfall of from 15 inches to over 100 inches per annum, but it is characteristically the cotton of low rainfall areas (say 20 inches—40 inches). The ecological distinction between *G. hirsutum* var. *marie-galante* and *G. barbadense* has been studied in the West Indian islands by Hutchinson (1943b and c). The former is the common cotton of the dry areas of the Spanish Main, the West Indies and north eastern South America. It is grown commercially in coastal Colombia, north Brazil, Haiti, and the Grenadines, and was formerly the basis of an extensive perennial crop in the West Indian islands (Hutchinson and Stephens, 1944). In dry areas throughout its range it occurs as a natural component of xerophytic scrub land vegetation, and from the ecological history of its wild habitats and the close relationship between the wild and commensal forms in each area, there is good reason to believe that the wild forms arose as escapes from cultivation.

The northern limit of the distribution is the Greater Antilles. From old accounts of the origin of the Sea Island crop it appears that *marie-galante* types were tried in South Carolina, but as would be expected with 'short day' cottons, they failed to fruit before the onset of winter. There is no record of successful introduction into the Old World.

The second line of spread of *G. hirsutum* was into eastern Mexico and Honduras, and thence northward along the coast. Here var. *punctatum* was developed, which is a smaller, bushier shrub than var. *marie-galante*. Two forms are known. The typical form is the cotton of the Maya country, and, it may be conjectured, was probably that cultivated by the Maya civilization. It is a mesophytic type in Central America, and is to be found all round the coasts of the Gulf of Mexico to Florida and the Bahamas, and in the Cayman Islands, Cuba, and Puerto Rico. In herbarium material the distinction between var. *punctatum* and var. *marie-galante* is by no means always clear, and a number of collections from the Lesser Antilles and the Spanish Main have been assigned to the former. From the extensive range of types from the Caribbean region growing in the C.R.S. collection, it is evident that var. *punctatum* does not occur south of the Greater Antilles, the Cayman Islands and British Hon-

duras. Cultivated forms include the Hopi cottons formerly utilized by the Indian tribes of the south western United States (Lewton 1912c) and the 'Fly-away' cotton of the Bahamás, which was the basis of the cotton cultivation of the early Bahamas settlers. Cotton from more or less spontaneous bushes is gathered for domestic use in Mexico and British Honduras, but in modern extensive cultivation var. *punctatum*, with its small bolls and low ginning outturn, cannot compete with the Uplands.

Cottons of this form have been extensively distributed in the Old World, and in many places have developed a high degree of tolerance of xerophytic conditions. In Africa, they have become more completely acclimatized than any other New World cotton. They are the common perennial cottons of the whole of the dry belt running across West Africa south of the Sahara, and provide the basis of the native cotton growing industry where it is too dry for Upland to thrive. Roberty (1938) reports that they soon take possession of abandoned Upland fields in the French Sudan. In other parts of Africa (Eritrea, British Somaliland, coastal Tanganyika, and Zanzibar) they are found as commensal plants, or in secondary growth on cultivated land. Acclimatization in Asia has not been so successful, but the 'Bourbon' component of the Nadam crop in the Madras Presidency is of this variety and is well established. Types of var. *punctatum* have run wild in Madagascar, the Philippines and northern Australia.

In the second form of var. *punctatum*, is included a considerable range of wild cottons from Central America and the Greater Antilles. In addition to the shrubby habit and water supply control of fruiting, characteristic of var. *punctatum*, these cottons are all adapted to xerophytic conditions, and generally possess sparse and irregular lint, small seeds, and a hard seed coat that results in delayed germination. They include *G. palmerii* Watt, of Central America, *G. ekmanianum* Wittmack, of Haiti, 'algodon brujo' (Hutchinson 1944) of Puerto Rico, and *G. taitense* Parl., formerly considered to be endemic in Polynesia. The form is highly variable, but appears to be better demarcated from the rest of var. *punctatum* than are the wild forms from the commensal and cultivated ones in var. *marie-galante*. In Puerto Rico, where both true var. *punctatum* and 'algodon brujo' occur, the ecological distinction between them is very marked (Hutchinson

1944), and a sharp distinction between the cultivated and commensal types and the wild *G. palmerii* is reported by Mauer (1930) from southern Mexico.

The annual Upland cottons of typical *G. hirsutum* are the cottons of northern continental Mexico, and the Cotton Belt of the United States, and it may be supposed that their isolation from the variable population of southern Mexico first took place in the Aztec state with the development of agriculture in plateau areas where the climate was unsuitable for the cultivation of perennials. Here, the control of fruiting by photoperiodism and by water balance has been lost, and cropping is determined by the node at which the first fruiting branch is formed, irrespective of the external environment.

The spread of Upland cottons into the present United States Cotton Belt began in the early seventeenth century (Kearney 1930). Ware (1936) distinguishes two main lines of development, first the green-seeded, small-bolled, prolific cottons centred in the eastern end of the cotton belt, and secondly the white-seeded, large-bolled, coarser types of the western States. The origin of the green-seeded types is uncertain, but from Mauer's (1930) description it is evident that their nearest relatives are in the area of high variability in southern Mexico. They probably represent a separate isolation from the population at the centre of variability. The white-seeded, big-bolled types, on the other hand, are in large measure descended from the cottons of the central Mexican plateau. When the boll weevil invaded the Cotton Belt the old green-seeded types, with their small bolls and long fruiting season, succumbed and were replaced by early big-bolled varieties. The effect on the quality of the American crop was serious, but American breeders working with hybrid material and new big-bolled stocks, such as Acala, from southern Mexico, set about combining the quality characteristics of the old types with the habit required to meet the new conditions, and a steady improvement in the quality of the crop has followed.

Intensive breeding work, including much hybridization both natural and artificial, has effectually prevented the separation of distinct types in the United States. The green-seeded prolific, and white-seeded big-boll, types are no more than the extremes of a series, the members of which are being constantly interbred. Divergence has occurred, however, between the Uplands of the



American crop and those acclimatized in the Old World. The Upland cottons of India were derived from two sources. The introductions of Upland Georgian and New Orleans types by the East India Company about the middle of the nineteenth century gave rise to the American cottons of Central and Northern India (see Return: Cotton [India] 1847, and Burt 1913). About 1905 officers of the Imperial Department of Agriculture in co-operation with business men in the Madras Presidency introduced acclimatized Upland types from Cambodia, Hanoi, and the Philippines (Main 1912). From this material the very successful 'Cambodia' cotton of the Madras Presidency has arisen, and has contributed to the genotype of much of the Upland material in Peninsular India, as far north as the Malwa plateau. Lewton (1925) has pointed out that the naturalized Upland types of the Philippines (*G. paniculatum* of Blanco 1837) were no doubt introduced direct from Mexico during the Spanish occupation. Mauer (1930) has recorded the presence of Cambodia-like types in southern Mexico, where even annual types may exhibit photoperiodism (see also Ware [1936] on the disturbance of the fruiting habit of certain southern Mexican Uplands when introduced into the United States). The excessive vegetative development of Madras Cambodia when grown in the long days of Sind (Dabral 1938) completes the evidence that Cambodia is a direct derivative of the tropical Uplands, and is not related to races acclimatized in the American Cotton Belt.

Though introduced by two distinct routes, the Upland Georgian and Cambodia cottons both belong to the old small-bolled, prolific, green-seeded type, and since their introduction into the Old World they have been subject to intense selection for the hairiness that is generally associated with resistance to the attacks of leaf-sucking insects (Macdonald, Ruston, and King, 1945). They are differentiated into three main agricultural races, the cottons of the northern alluviums (Cawnpore, Punjab, and Sind Americans), the Upland Georgians of Peninsular India (Malwa Upland, Buri, Malan, Dharwar American, and the Upland component of Umri Bani), and the Cambodias.

Though the Upland cottons of Africa were introduced more recently, they are mostly descended from pre-boll weevil American long staple varieties, and selection for prolific fruiting to counter bollworm attacks, and for the hairiness usually asso-

ciated with jassid resistance, has emphasized their similarity to the acclimatized Indian types. Differentiation into distinct agricultural races is already in progress, the rather lower quality, compact, rapid-fruited U<sub>4</sub> type having been isolated for jassid resistance from the variable, but predominantly high quality, lax, slower-fruited, more jassid-susceptible 'Lake type' of Uganda, Tanganyika, and Nyasaland.

Upland strains collected in Persia by Ansari (1940) are of the same intensely hairy, rather small-bolled, prolific type. Acclimatization in the Old World, therefore, has favoured one general type which is very distinct from the modern varieties of the American Cotton Belt.

A newer area of expansion of Upland cottons is in the State of Sao Paulo in Brazil and the Chaco region of the Argentine. Much interest is taken in the introduction of established varieties from the United States and elsewhere, but the beginnings of the emergence of a locally adapted race is shown by the success of the 'Chaco' type and selections from it in the Argentine. In Russia, also, a great expansion of Upland cottons has taken place in recent years, and without doubt a local geographic race will appear in due course.

The differentiation of the Upland cottons in some of the recent extensions to their range will be considerably affected by hybridization with vars. *punctatum* and *marie-galante*. Overlapping with var. *punctatum* occurs in the Sudan region, where the latter has become established as the cotton of native small-scale cultivation, and Uplands are grown extensively as an export crop. Among the West African types in the C.R.S. collection is to be found a range from typical var. *punctatum*, similar to the Central American form, to small, early sub-shrubs with no vegetative branches, that are distinguishable from pure Uplands only by their small leaves and bolls. Reference has been made in Part I to Harland's (1939) account of the consequences of hybridization between Upland and var. *marie-galante* in north Brazil. The value of such hybrid material to the plant breeder engaged in producing locally adapted cottons in the areas where the varieties of *G. hirsutum* overlap is very considerable.

The extension of the Uplands from a comparatively small area in Mexico until they occupy an important place in nearly every cotton-growing country, and produce well over half the world's crop, is one of the most remarkable chapters in the

history of cotton, and the development of fresh geographical races will provide a most instructive demonstration of the differentiation of an expanding species in response to new environments and fresh isolation barriers.

The greater part of the cotton-growing area of the New World is, and always has been, sparsely populated. Local concentrations of human population occurred in the areas occupied by the pre-Columbian civilizations, and in the large crop populations that accompanied them there arose the variability from which the modern New World cottons were differentiated. In the last two centuries the human and crop populations of the United States Cotton Belt have increased enormously, and the major adaptive trend of the Old World—the replacement of perennials by annual selections—has come into play in the establishment of Uplands in *G. hirsutum* and Sea Islands in *G. barbadense*. In most of the rest of the New World range, cotton is still a perennial shrub. In general, it is a commensal plant which provides the raw material for the homespun fabrics of the scanty human population. Where extensive agriculture has been introduced, the local commensal cottons have provided the foundation stock for the commercial crop, and it is only as the agricultural system is developed to meet the increasing demands of a developing community that the selective forces favouring the annual habit come into action. Thus it is that in the coastal areas of north Brazil and Peru, hybrid populations between Upland and *G. hirsutum* var. *marie-galante* in the one case, and between the Tanguis perennial and Egyptian annual races of *G. barbadense* in the other, hold out the promise of locally adapted annual types for the future.

In conclusion, attention may be drawn to the need for a comprehensive comparative study of the measurable characters of cotton lint. The genetical and botanical studies here reported have demonstrated the central place occupied by human selection in the evolutionary history of the genus. Yet knowledge of the range of lint characters available, and their distribution between the different species, varieties, and races of the linted cottons, is extremely limited. Some information has been published by Hutchinson and Govande (1938) for Indian cottons, and by Hutchinson (1943d) and Hutchinson and Manning (1945) for the Sea Island group. Further data are available in technological literature, but in many cases it is impossible to

correlate them with the modern classification of the species. A comprehensive study of modern cottons, together with an examination of material from the fabrics of ancient India and Peru, should go far to elucidate the history of the development of quality in cotton.

## PART FOUR

### THE SIGNIFICANCE OF 'GOSSYPIUM' IN EVOLUTIONARY STUDIES

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#### I. INTRODUCTION

**G**OSSYPIUM has the great advantage for evolutionary studies that it embraces within the limits of what is almost certainly a monophyletic group, species of extremely different biological status and evolutionary history. Among the wild species, changes in taxonomy with increasing knowledge have been very slight, and the classification given in Part I is substantially the same as that of the original authors of the species, except in so far as certain minor genera have been sunk in *Gossypium*. Morphological distinctions are large, and are matched by crossing barriers or cytological differentiation. By contrast, among the cultivated species there has been a great reduction in the number of species accepted as valid. The five species included in the two **Sections** comprising the linted cottons in Part I are represented by twenty-one species in Watt's (1907) monograph, and to them he added another eleven in later papers; and these constitute but one author's opinion of the ramifications of the classification of the cultivated cottons before the application of genetic analysis to the problem. Parallel with the vast range of variability which has given rise to taxonomic confusion, the morphological differences between true species are comparatively small, and crossing barriers and cytological differentiation are confined to those consequent on polyploidy.

Judged either on size of populations, area at present occupied, or extent of recent increases in range, the linted cottons must be regarded as highly successful from the standpoint of evolutionary progress, whereas the wild species are, with the possible exception of *G. anomalum*, static or even relic in status. The origin of the linted from the wild species, the evolutionary mechanism through which their success has been achieved, and the changes in genetic constitution that have been associated with it, are matters of fundamental importance to students of evolution, and throw light on such basic problems as the origin of new characters, the significance of polyploidy, and the interrelations of variability and dispersion.

## II. THE DEVELOPMENT OF NEW CHARACTERS AND THE SIGNIFICANCE OF POLYPLOIDY

THE success of the cottons has resulted from the evolution of two new characters, convoluted lint hairs and the annual habit. In both, the basic change involved is comparatively simple, and depended on the exploitation of potentialities already existing in the parent material. The most instructive features of their development are the conditions which made their emergence possible, and the genetic changes which were their necessary accompaniment if the new types were to achieve biological success.

Given the spiral arrangement of the cellulose fibrillae in the unconvoluted seed hair, the formation of lint following a mutation causing reduction in the amount of cellulose deposited, might occur at any time. Linted mutants may have occurred countless times in the history of the wild species of *Gossypium* before one arose at a time and place where civilized man, on the lookout for new textile materials, or even merely for novelties to ornament his older textiles, could recognize its attraction and take it into cultivation. Successful evolutionary change depends, in fact, on a fortunate coincidence of the emergence of a new character with the occurrence of an environmental change which makes it advantageous.

The first advance along the new evolutionary path having been made, new selective forces governed further progress. Given convolutions, the seed hairs on a wild *Gossypium* can be spun, but they are short, few in number, and firmly attached to the seed, and great patience would be required to remove sufficient even to ornament another fabric. Before cotton could become established as an independent textile, it had to be readily available in quantity. Increase in capsule size and seed size, and greater density of hairs on the seed coat, and to some extent improvement in hair length, were therefore essential to the establishment of lint as a biological success. Changes of this magnitude involve nothing less than an extensive rebuilding

of the genotype. From Silow's (1941) analysis of the genotypic differences between *G. anomalum* and the cultivated diploid cottons, it is evident that this reorganization was accomplished by the accumulation of gene differences, and not by any 'macro-evolutionary' change of the type postulated by Goldschmidt (1940). The origin of new characters may therefore be ascribed, first to the occurrence of mutations, normally of no value or even deleterious, under new conditions where they confer an initial advantage, and secondly to the existence in, or acquisition by, the mutant stock of a store of gene variability sufficient to allow adaptive response to selection of such magnitude as virtually to reconstruct the genotype around the new character. Such a genotypic reorganization can best be observed in the development of annuals from perennials among the cultivated cottons. Here the process is not yet complete, and many of the intermediate stages still exist.

The fruiting of a perennial cotton is controlled by a complex of characters. The most easily observed component is the node at which the first fruiting branch appears, and this very largely controls the onset of the reproductive phase in the first season. For successful cropping over a period of years, however, some mechanism is required by which a reproductive periodicity can be set up in conformity with the seasons. This is usually achieved in the wild species and the cultivated perennials by photoperiodicity, or by water supply control of bud shedding. Many perennials carry both controls, so that the development of fruiting branches only occurs during the period of the year when the days are short, and the flower buds then produced are only brought to maturity if the weather is dry. In the development of the annual habit, selection is, of course, for early fruiting in the first season, behaviour in later seasons being immaterial, as the plant does not survive long enough for its expression. Provided there is no alteration in the relation between the march of the seasons and the development of the plant, functionally annual cottons may be established simply by the selection of types forming the first fruiting branch low down on the main stem, and the photoperiodic response, or the facultative shedding habit, may persist. An example of the former is the existence of the photoperiodic habit among the tropical types of *G. hirsutum*, and of the latter the occurrence of facultative shedding in many of the Western Indian races of *G. herbaceum* var. *acerifolium*.

Nevertheless, there exists a very definite association between the characters controlling the fruiting of perennials, so that the establishment of the really early annual cottons has involved not only the loss of the periodicity controls, but also the subordination of the whole plant development to the demand for a quick and copious crop. Consequently, whereas in some more recent annual selections such as Sea Island, a well treated plant will persist for some years, the most advanced annual types such as American Uplands or *G. arboreum* race *sinense* suffer a very heavy mortality at the end of the first season, and die out altogether within a short period.

The genetic processes involved in the development of lint are closely parallel to those which Mangelsdorf and Reeves (1939) believe were concerned in the establishment of the maize ear. A single mutation provided the focus round which the whole genotype was reorganized, and a South American grass transformed into a unique cereal plant, which is no longer capable of surviving in the wild. Similarly, the establishment of the non-shattering rachis in wheat and the non-articulate grain base in oats were fundamental steps in the process of domestication. Yet a vast further differentiation was required to transform the wild grasses into the crop plants of modern agriculture, and speltoid and fatuoid mutants in wheat and oats are no nearer their wild prototypes than tunicate maize is to the grass from which it sprang.

The simple gene mutations which make possible the development of new characters have a parallel in the occurrence of polyploidy, which has been of considerable importance in speciation in the plant kingdom. Its significance has been discussed by Dobzhansky (1941) and Stebbins (1940), and they have concluded that though it has played a considerable part in species formation in many groups, its value is chiefly as a short term evolutionary mechanism, and in the long run polyploids are unlikely to originate new major evolutionary lines. This commonly accepted view of the evolutionary prospects of polyploidy follows from the belief that diversification in them is confined to 'new variations on an old theme' (Stebbins 1940), and that the shelter to destructive mutations provided by gene duplication 'must inexorably lead to a progressive deterioration of the germ plasm' (Dobzhansky 1941). Among crop plants polyploids possess the characteristics of high vari-



ability, extensive differentiation from their wild prototypes, and great range and adaptability, that are usually associated with evolutionary success, and it is here suggested that far from being variations of no long-term significance, they lie on a main line of evolutionary advance. Like the occurrence of lint in *Gossypium* and the non-tunicate mutant in the ancestral *Zea*, the occurrence of polyploidy does no more than provide a focus round which genotypic differentiation can proceed. Once the basic change has been established, further development is dependent on genetic diversity, and the diversity available in polyploid material is not in dispute. In this respect Stebbins (1940) himself has drawn attention to the variability arising by recombination in such polyploid complexes as exist in *Crepis* and *Paeonia*. Given variability new characters can, and do, arise irrespective of the ploidy of the stock, as for instance the annual habit in *Gossypium*, which has been developed independently in the cottons of the Old and New Worlds, or may emerge in the polyploid species of a genus only, as is the case with the non-shattering rachis in wheat.

The probable course of development of the germ plasm in a new polyploid may be considered, to see whether there is justification for the conclusion that the sheltering of deleterious mutants by their normal homologues will lead to progressive deterioration. In the first instance, all genes will be duplicated which are carried by both parental species. In autopolyploids duplication will be complete. In allopolyploids its extent will be in general inversely proportional to the extent of the differentiation between the parental species, and if this is large, masking is likely to be small from the beginning.

The fate of loci at which the presence of one dominant gene is sufficient to give full normal behaviour (i.e. complete masking) may be illustrated from the genetics of chlorophyll deficiency in New World cottons. Harland (1932b) showed that many strains of *G. hirsutum* are dimeric for dominant normal genes (**Chl<sub>1</sub>** and **Chl<sub>2</sub>** on Hutchinson and Silow's [1939] notation), and those that are monomeric carry **Chl<sub>2</sub>** only. It has recently been proved (Hutchinson, 1946) that *G. hirsutum* var *punctatum* is frequently monomeric, carrying **Chl<sub>1</sub>**. Further, all *G. barbadense* strains tested (Harland 1932b) were monomeric, carrying **Chl<sub>1</sub>**. There has, therefore, been extensive loss of duplication, which appears to have been at random, since the mono-

meric condition has been established with different **Chl** genes in two varieties of the same species. Once the monomeric condition is established, however, the effect of recurrent mutation is balanced by selection against recessive mutant segregates which, being no longer masked, are as deleterious as the corresponding mutant recessives in a diploid cotton. Hence, the genetic behaviour of a chlorophyll deficient mutant in a monomeric Uganda Upland cotton (Hutchinson, 1946) was exactly parallel to that reported by Hutchinson and Bhola Nath (1938) in a *G. arboreum* strain. The deterioration of the germ plasm cannot be said to be progressive, since the balance between mutation and selection is re-established as soon as the monomeric condition is reached.

The occurrence of the monomeric condition in some genes of a polyploid may also be the result of the genotypic constitution of the parental species. In corolla colour and pollen colour in cotton, at least as many independent genes are known in the Asiatic diploids as in the allopolyploids, and it is likely that the American diploid ancestor carried no dominants at the homologous loci. In lint colour, on the other hand, the Asiatic parent may well have lacked dominants, but the allopolyploid would receive *both brown and green* colour genes from the American parent. In these cases the diploid condition is characteristic of the polyploid *ab initio*, but there is no reason to postulate that some loci are missing from one set, since by the use of different diploid parents, allopolyploids carrying dominants in both genomes could no doubt be synthesized.

So far, only those cases have been considered in which the occurrence of a gene at one of two duplicate loci has the same effect as at two, and it has been shown that an equilibrium will be reached with the re-establishment of the functionally diploid condition, when selective *elimination of degenerative mutants* again becomes effective. Mutants at loci carrying genes which are not simplex-sufficient, on the other hand, will be subject to control by selection from the start, and there is much experimental evidence for the view that this is a commoner situation than masking by duplicates. A good illustration is provided by the duplicate anthocyanin—'short branch' chromosome segments studied in New World cottons by Silow (1946). With neither of these pairs of duplicated loci does any masking occur. In the anthocyanin series, the alleles at both **R**<sub>1</sub> and **R**<sub>2</sub> in the

various species concerned are so different that there is no true duplication of alleles in the allopolyploid. Dominance between alleles is rare, since they generally affect different parts of the anthocyanin pattern, and therefore are more or less independent in their effects. The rate of mutation varies with the genotype, and in some cases is so high as to lead to the virtual elimination of an allele, as for example  $R_2^{45}$  from the Upland cottons. The absence of masking in this case, therefore, is due to the extensive range of alleles available, the frequency with which their effects are independent, and the high rate of mutation in certain genotypes.

The normal alleles of cluster and short branch are just the kind which would be expected to mask a recessive at the homologous locus, but the single recessive in each case is fully expressed. In an interspecific hybrid between the two single recessives, Silow obtained in  $F_2$  approximately 1 normal in 16, and a wide range of expression of short branch in the remainder, indicating that in such material, expression of short branch was roughly proportional to gene dosage. A similar situation has been reported in a comparison of diploid and autotetraploid tomato carried out by Sansome (1933). He showed that genes exhibiting full dominance in the diploid gave a range of expression varying with dosage in the tetraploid, so that instead of the two classes expected on the masking theory, he obtained either a number of classes separated only by small intervals, or an almost continuous, unclassifiable array.

Where dominance is incomplete in the diploids, the position in the polyploid is likely to be even more complex, and studies in experimental taxonomy (Gregor 1938) and plant breeding (Hutchinson *et al.* 1938) have shown that high dominance in quantitative characters subject to polygenic control is exceptional. Variability arising in such characters, therefore, will be immediately subject to control by selection, and as has been shown above, it is this type of variation which is of primary importance in evolutionary differentiation.

Harland (1936a) has suggested that where genes have pleiotropic effects, polyploidy might permit divergence in function, leading to elimination of masking, and restoration of an effectively 'diploid' condition. Such divergence is extremely difficult to detect, since effective divergence would eliminate the only satisfactory evidence of homology. Nevertheless, the first stages

of such a divergence may be observed in the anthocyanin series, where no exactly duplicate alleles are known at the  $R_1$  and  $R_2$  loci, and masking is consequently absent. A further stage may be observed in *G. anomalum*, in which the anthocyanin locus, but not the whole genom, is duplicated relative to the Old World cottons. In the latter, one type of petal spot results from the complementary action of the ghost spot and spotless alleles at the  $R_2$  locus. In *G. anomalum* a similar complementary effect occurs, but the two alleles are at independent loci and, but for the homology with the cottons, would be regarded as giving a basic colour gene plus a pattern gene type of action. Changes in gene function associated with polyploidy have been reported by Stephens (1944a and unpublished), who has shown that the leaf shape multiple allelomorph series in the New World cottons affects bract tothing, whereas the homologous series in the Old World cottons does not. The effect of the new balance created by the association of the A and D genomes is shown in the  $F_1$  of *G. arboreum*  $\times$  *G. thurberi* in which the bracts are deeply gashed, though in both parental species they are entire or nearly so.

Enough has been said to show that the possibilities of variation in a polyploid are no less than in a diploid, and that much of the variability arising by mutation will be subject to selection from the beginning. The general tendency throughout is towards a restoration of the diploid condition, which is in fact the state of affairs that has been found in all old established polyploids that have been subjected to genetic analysis. This is achieved by various means. First, the new balance in the polyploid may be such that masking is absent from the beginning, as with various characters in Sansome's polyploid tomatoes. Secondly, masking may be lost by the substitution of a recessive at one locus, as in chlorophyll deficiency in cotton and probably the normal allele of mammoth in *Nicotiana tabacum* studied by Clausen (1941). There is no evidence that the locus is lost in such cases, and that the recessive allele may be by no means inactive is shown by Stephens' (1944c and g) analysis of leaf shape in the New World cottons, from which it appears that the shape series is such as would be expected from a combination of the Asiatic series of alleles with an allele for entire leaf at the duplicate locus.

Beside the effects of the new balance, and of gene substitution, however, some more fundamental differentiation of the

germ plasm must be involved to account for such phenomena as the lower cross homology reported by Clausen (1941) between the sub-genoms in haploid *Nicotiana tabacum* than in the *N. sylvestris* x *N. tomentosiformis* hybrid. Clausen (1941) concludes that the sub-genoms of the established amphidiploid are no longer self-sufficient, and from a comparison of haploid *G. barbadense* with hybrids between Old World cottons and American wild species, it is evident that the same applies in *Gossypium*. In both genera, pairing between the sub-genoms of the amphidiploid and homologous genoms from diploid species, is such as to rule out major structural change, or losses of germ plasm, as an important factor in the loss of genom independence, and the most likely interpretation is that differentiation has resulted in some kind of division of function between them.

Such functional differentiation is in no sense deterioration of the germ plasm, and even where a new balance is set up following changes in chromosome number, such as must have occurred in the establishment of the Pomoideae, the fact that the new balance is maintained shows that the process was not degenerative.

The best example of progressive deterioration of the germ plasm is to be found not in polyploids, but in bisexual animals, in many of which the 'differential segment' (Darlington 1939) of the Y chromosome has become empty (Muller 1932) by just this process of accumulation of sheltered mutants which has been supposed to cause deterioration in polyploids. In animals the shelter is provided by the X chromosome, and damage to the organism is prevented by the elimination of mutants in the sheltering X by selection. That the sheltering of deleterious mutants does no irreparable harm to an organism will be evident from consideration of the breeding system of maize, in which outcrossing acts as a sheltering mechanism by increasing the chances of survival of deleterious recessives in the heterozygous condition. The amount of 'damaged' germ plasm carried by maize is very large, but the success of the plant is sufficient to prove that a satisfactory equilibrium is maintained between the rate of occurrence of deleterious mutants and their elimination by selection. A masking mechanism, in fact, does no more than increase the hidden reserve of variability, and degeneration will be checked when a balance is struck between mutation and selective elimination.

Evidently the evolutionary potentialities of a young polyploid will rapidly approach those of a diploid, and there only remain for consideration the conditions under which polyploidy is likely to be a biological success. When it first arises a polyploid will be under an even greater disadvantage than a diploid carrying a new and potentially successful character. Being represented initially by a single individual, it will lack the variability necessary for adaptive response to selection, and will in addition be cut off by a sterility barrier from accessions of variability from the parental species, except in polyploid complexes, such as those discussed by Stebbins (1940), where several interfertile polyploids have arisen side by side. Stebbins (1940) has pointed out that polyploids are generally dominant in areas that have recently become available for colonization, or in which great environmental changes have occurred, while diploids tend to predominate where stable conditions have long persisted. It also seems a fair generalization that successful polyploids usually exceed their parents in general vigour. It may then be suggested that while stable conditions persist, a new polyploid, lacking variability, and differing somewhat from the locally adapted diploid in consequence of the new genotypic balance established, will generally be unable to compete with the parental type on account of the slowness of its response to selection. Where vast new habitats are opened up, as with the retreat of the ice after the glacial periods, or with the radical alteration in vegetation caused by agricultural practice, the pre-existing diploids will probably be no better adapted to the new conditions than their polyploid derivatives, and their greater plasticity will be balanced by the vigour of the polyploids. Once the latter are established and widely spread their plasticity will increase with the increase of the genetic variance, and their initial disadvantage in this respect will be overcome.

The observation that polyploidy is associated with species differentiation, but not to any great extent with the establishment of major evolutionary lines, now becomes explicable. There have been in recent times two great changes in the gross environmental factors affecting the plant kingdom, the extermination and recolonization associated with the Ice Age, and the great changes in vegetation that have followed from the spread of cultivation. These changes have been followed by the spread of polyploids, in the North Temperate flora on the one

hand, and in the categories of plants (crop plants, weeds, and the flora of pastures, hedgerows, and waste places) associated with man's agricultural activities on the other. Differentiation in these newly opened environments has given rise to extensive speciation, but insufficient time has elapsed for the establishment of higher categories.

### III. THE NATURE OF GENETIC VARIABILITY AND THE ORIGIN OF DISCONTINUITY

THE demonstration that new characters of evolutionary significance arise in the same kind of variability as causes the diversity observed in natural and cultivated plant populations, simplifies the discussion of variability enormously. If the basic change responsible for the origin of lint is no greater than has been observed to occur by mutation in pedigree culture, and the difference between the wild and cultivated species has been built up around the lint character by manifold gene substitutions, there is no need to consider the possibility of species differentiation by 'macro-mutational' changes. The whole problem of variability, from the diversity of crop populations to the discontinuous variation characteristic of species groups, may be analysed in terms of the kinds of mutational change observed in genetic experiments.

Apart from changes which involve whole chromosomes or whole sets of chromosomes, mutational changes in the widest sense may involve anything from a major change in order or position of a group of linked genes in the chromosome, to a 'point mutation' affecting only a single locus. These changes form a closely graded series, so that although there is probably a difference in kind between 'intragenic' and 'intergenic' changes (Dobzhansky 1941), they do not fall into distinct classes on their genetic behaviour. The difficulty of drawing a dividing line between them is illustrated by the work of Silow and Yu (1941) on the anthocyanin allelomorph series in Asiatic cottons. It was found that this long allelomorph series included members whose origin could as easily be explained by rearrangement of sub-units within the locus as by new point mutations. More recently Silow (unpublished) has found indisputable evidence of the occurrence of such rearrangement by crossing-over. It is possible, therefore, that there is a continuous intergrading series between the gross structural change, visible at meiosis as abnormal conjugation of chromosomes, anaphase bridges, etc.,



and the point mutation which involves, so far as can be discovered, no more than a single locus. Quite apart from their primary phenotypic effects, the survival value of the two extremes of the mutation range will be very different on account of their effects on gamete formation. Structural changes which are of sufficient magnitude to modify normal meiosis usually lead to the formation of a proportion of inviable gametes. They are therefore at a selective disadvantage. Smaller changes, except in the special case of lethal genes, or deficiencies, do not lessen fertility. Normal meiosis is followed by normal gamete production and the 'mutation' behaves subsequently as a genetic unit in breeding tests. There seems to be no *a priori* reason for supposing that there is any definite relation between size of change and frequency of occurrence. The chances of survival of such changes, however, will be roughly inversely proportional to their size. Large structural changes causing considerable reduction in fertility when heterozygous, will only spread by replacement when they have been established in the homozygous condition, and moreover, only one at a time, unless, of course, they possess a powerful selective advantage for other reasons. In general Wright's (1941) conclusion regarding reciprocal translocations probably applies, that 'such fixation can hardly occur under exclusive sexual reproduction except in a species in which there are numerous isolated populations that pass through phases of extreme reduction in numbers'. Changes causing no reduction in fertility, such as small inversions, may 'float' (Darlington 1939) in a population, but in so far as they reduce crossing over in that chromosome they will reduce the number of recombination products available for selection and slow down adaptive response. It may be concluded that such minor changes are only likely to 'float' in a population in which gene recombination is unimportant, that is to say, in an organism in equilibrium with a fairly stable environment. Where rapid adaptive response to changing environmental conditions is required, any factors reducing the rate of recombination will be at a disadvantage and will be eliminated.

Beasley (1942) has pointed out that chromosome differentiation is an essential prerequisite to allopolyploidy, since without it, pairing between chromosomes of different genomes will lead to meiotic disturbances. It is not at all clear, however, that gross structural changes are necessary to bring about the required

differentiation. The capacity of two originally homologous, but now differentiated, chromosomes to pair, is not an 'all or none' matter. It is at a maximum when each potential partner is haploid, and at a minimum when one partner is in the diploid condition. 'Differential affinity' of this type is illustrated elsewhere (Stephens 1942, 1944c) by comparing the numbers of bivalents found by Skovsted (1937) in interspecific AD diploid hybrids with the numbers of trivalents found in the corresponding AAD triploids. Gross structural changes would appear to be too infrequent, and in fact, too crude a mechanism, to condition pairing affinity, and it seems likely that small structural changes which are undetectable cytologically are chiefly concerned.

The distribution of chromosome differentiation in *Gossypium* is as would be expected from these considerations. In both groups of cultivated cottons, in which adaptive change has been rapid and populations large, chromosome homology is high. Among the wild species, in which populations are small, and which give every indication of being in close equilibrium with stable environmental conditions, major structural differences are common, and the lack of homology that might result from the gradual accumulation of small inversions is widespread.

Wright's (1941) analysis of the chance of establishment of a reciprocal translocation emphasizes the fortuitous nature of major structural alterations, and Silow's (1941) demonstration that the species difference between *G. anomalum* and the Old World cottons is of the same kind as that between *G. arboreum* and *G. herbaceum*, shows that such major changes are not among the essentials of species formation, though they may play a large part in consolidating species barriers. It is by the accumulation of minor changes that differentiation proceeds. In a successful species with a large population, these provide a store of variability in which manifold recombinations are possible, and through which adaptive response to selection goes on without catastrophic changes in population size. Evidently, divergent evolution leading to species formation can only take place in such populations following isolation of some kind, and comparisons of the extent of varietal differentiation in *G. herbaceum* versus *G. arboreum* on the one hand, and in *G. hirsutum* versus *G. barbadense* on the other, provide good illustrations of the function of geographical isolation in this respect. In a popula-

tion which is not subdivided by physical barriers, gene exchange prevents the establishment of discontinuities. Where the species is divided into discontinuous groups, character differences arise between them, and gradually character complexes arise that impart a genuine varietal distinction to the isolated geographical races. The existence of all stages in this differentiation, from the incipient separation between geographical races to the full species distinction, has been demonstrated in the cultivated cottons.

In view of their great importance, it is worth considering how these small differences arise, and by what system they are maintained. The variability of unselected populations of crop plants is so high as to make cultivated plants as a whole a notoriously difficult group for the taxonomist. Though high variability is now generally accepted as an intrinsic feature of their evolutionary status, and much information has been collected on its distribution (Vavilov 1935), the problem of its origin has received less attention than it deserves. Crop plants have been developed from wild plants with comparatively low variability, and many cultivated species, such as those dependent on the origin of a new character (e.g. cotton lint) for their value to man, and those which arose by polyploidy, must be descended from single, or at most very few, original plants. Evidently their present diversity cannot have existed as gene differences in these very small original populations, and it is necessary to consider whether it can be accounted for by what is known of the rate at which variability can be built up.

Three factors govern the accumulation of variability in an organism: the mutation rate, in which may be included the rate of release of hidden variability from balanced polygenic combinations (Mather 1941), the adaptive balance between the organism and the environment, and the size of the population. Timofeeff-Ressovsky (1940) has estimated that from 1 to 10 per cent of all gametes contain a new mutant. Such a rate of acquisition of variability would permit of a very rapid increase in diversity if it could be shown that any considerable proportion of it survived in the breeding stock. In a perfectly adapted organism, obviously all mutational changes would be deleterious. Conversely, the less perfect the fit of organism to environment, the greater the chance of a favourable variant arising. With any considerable change in the environment, with a conse-

quent deterioration in the adaptive balance, new variability that would have been disadvantageous under former conditions will in many cases be good enough to persist, and form a basis for improvement. A temporary increase in variability may therefore be expected to follow any disturbance in the balance between genotype and environment. Where an increase in population occurs, as in the colonization of a new situation, Fisher (1930) has shown that neutral mutations, or even those at a slight disadvantage, have a chance of avoiding extinction, and will also contribute to the variability, and finally a large population maintains a greater store of variability than a small one. Hence in a successful organism, the acquisition of variability is cumulative, each success leading to an increment in the stock of variability upon which further success depends.

The conditions of cultivation add other factors favouring the conservation of variability. Inter-species competition is cut down by clearing and weeding, and intra-species competition is controlled by spacing. The elimination of competing vegetation makes possible establishment in a vastly wider range of ecological situations than would be open to a similar species in the wild. In effect, cultivation causes a relaxation of the selective forces operating on an organism, followed by their diversification as it spreads under cultivation into new environments.

Some evidence is available which indicates that these factors are adequate to build up the diversity observed in crop plants. Goodale (1937) has discussed in detail two selection experiments, one by Payne on bristle number in *Drosophila* and one by himself on 'white head dot' in the mouse, in which a response to selection was obtained out of all proportion to the variability of the initial stocks. The foundation material was a single pair in the *Drosophila* material, and five individuals in the mouse experiment, so that the initial genotypic stock was extremely limited in both. Goodale's conclusion is unavoidable that the limits to response to selection must at least be very much wider than is generally supposed. Payne believed that variability in bristle number had arisen in his *Drosophila* stock by mutation during the course of the experiment. From the crossing behaviour of the selected mice Goodale concluded that what Mather (1941) has recently called a 'polygene complex' had been built up, which, within the limits imposed by crossing over, behaved as a single Mendelian unit.

In each of these experiments a single character was subjected to selection. Nevertheless, the response to such selection may extend to many characters beside the one studied, as has been shown by MacArthur (1944) in his analysis of the effects, on related characters, of selection for body size in mice. The general balance between the different changes he observed bears a striking resemblance to the type of balanced adaptive response that occurs under natural selection. That such general selection for adaptive response may also be effective in populations of very limited ancestry is shown by Hutchinson and Manning's (1943) analysis of the effect of selection on U<sub>4</sub> cotton, an Upland variety descended from a single plant selection made in 1924-5. The original U<sub>4</sub> progeny was variable, and the breeding system adopted was such as to conserve the variability, but even so, the extent of the differentiation achieved in adaptation to local conditions is remarkable, and current reports indicate that sufficient variability still remains to provide attractive material for the plant breeder.

#### IV. THE EVOLUTIONARY PROSPECTS OF A CROP PLANT

THE immediate consequences of cultivation, for any plant species, are a great increase in population, and a radical change in the impact of selection. Considering population size first, not only is the actual number of plants in the species greatly multiplied, but isolation within the species is much reduced, and the size of interbreeding groups correspondingly increased. This results not only from the effective continuity of populations of extensively cultivated crop plants, but also from the free seed exchange that goes on in agricultural communities. In consequence, the establishment of isolated subpopulations in which chance divergence (Wright 1940) might supplement adaptive change in causing racial differentiation, is less common than in wild plants.

This effective panmixia (Wright 1940) is more pronounced now than formerly, when transport difficulties made distance a much more effective barrier to interchange than it is to-day. The easy intercourse of modern times has had two important effects on crop plant speciation. In the first place, groups that were differentiating in the comparative isolation provided by distance are now interbreeding. This is particularly pronounced in *G. arboreum*, where easy exchange of seed has led to the spread of commercially desirable types until the racial boundaries overlap. Other examples are provided by the spread of the Upland cottons. *G. hirsutum* var. *marie-galante* in northern Brazil and *G. hirsutum* var. *punctatum* in French Africa have been brought into contact with more recently introduced Upland cottons, and hybrid stocks have arisen in which the varietal distinctions have been broken down. Here, reversion to panmixia has effectively stopped the speciation process, but in so far as it has released a further store of variability on which selection will act, it has contributed to the evolutionary advance of the species. Where no species barrier has been set up, therefore, the highest degree of differentiation that is now likely to arise in a cultivated

crop is the separation of geographical and ecological races. In the Upland cottons, for example, the exacting demands of the Indian climate have resulted in the development of a local type with which new introductions from elsewhere cannot compete. The Indian type is therefore fairly well isolated by a combination of geographical and ecological factors. Nevertheless, the use of introduced types in hybridization work has already begun, and is likely to increase. Gene exchange in such stocks will effectively limit differentiation to that required to meet the rigorous demands of the Indian environment, and fortuitous differences between Indian and other races of Upland cottons are likely to break down and disappear.

The second important effect of free intercourse is on the further differentiation of species separated by genetic barriers built up in isolation. Where such species have been brought together by the spread of cultivation they are not infrequently grown in mixed crops, and abundant opportunities occur for natural crossing. Where the barrier to interbreeding is incomplete there will be some loss of reproductive efficiency as a result of hybridization. Consequently any mechanism making the barrier more complete will be favoured (see Dobzhansky 1941). Stephens (1946) has shown how such an intensification of the species barrier is developing in the New World cottons with the spread of the 'corky' mechanism, and from a re-examination of Hutchinson's (1932) data, he has shown that an isolating mechanism depending on alleles at a single locus can become so complete as to give empty seeds on crossing. The behaviour of the cottons in areas of overlap, then, shows that whereas contact tends to break down separations below the level at which a species barrier arises, above that level it tends to enhance them and make the barrier complete.

The selective forces operating on a cultivated crop are widely different from those effective in the wild. The removal of inter-species competition by cultivation and weeding reduces the pressure of selection enormously in the early stages, and leads later to the intensification of intra-specific competition. This difference doubtless has an important effect on variability, powerful interspecific competition tending to establish a uniform 'wild type' very closely adapted to a particular ecological situation, whereas in the absence of other competing species, a wider range of situations is open, and competition is likely to

be less severe in a group of slightly different types than in a uniform population. Hence arises the situation observed by Hutchinson *et al.* (1938) in analyses of unselected crops in Central India, in which 'the fittest population is a mixture of types'.

A further consequence of the change in selective forces accompanying domestication has been the progressive loss from the commercial cottons of characters essential for successful survival in natural vegetation. Certain features characteristic of the adaptive response of the wild species, such as ability to withstand drought, intolerance of shade and competition in the seedling stage, have persisted in the most advanced cultivated cottons. Others, such as a hard seed coat and delayed germination, were among the first to be eliminated by selection for agricultural suitability. Still others, such as the perennial habit, facultative shedding, and the photo-periodic response, persist in the less advanced of the cultivated cottons, but are not to be found among the most specialized crop varieties. The chance of successful re-establishment in natural vegetation is in almost direct proportion to the number of these primitive characters retained. There is no record of successful reversion to the wild in the specialized early annual cottons of either the Old or New Worlds. Among the perennials, however, establishment in natural vegetation has been successfully accomplished in all species, and the wild derivatives combine the perennial habit with facultative shedding or photoperiodicity, and generally with a hard seed coat and delayed germination.

It may be argued that specialization to the extent of eliminating all possibility of reversion to the wild is 'blind alley' evolution. Nevertheless, there seems no reason to regard specialization as a prelude to evolutionary disaster in crop plants. The wide range of ecological conditions to meet which local strains have been developed, the enormous size of the interbreeding populations, and the extent to which, especially in modern times, material is exchanged between widely separated areas, minimizes the chances of irrevocable loss of valuable genetic material.

The success with which genes for disease resistance have been sought out and re-established in crop varieties in recent years shows how extensively genes governing characters long neglected, persist in crop populations. Moreover, adaptation to meet the conditions of a man-made environment may now be regarded as



the major line of evolutionary advance if, as seems certain, man is to exercise a steadily increasing control over the earth's vegetation. Consideration of the important place occupied in the world's fauna and flora, not only by domestic animals and crop and forage plants, but also by weeds, plants colonizing waste and abandoned land, pests and disease organisms, will make manifest the far-reaching influence of the dominance of man on the course of evolution.

Much instructive information may be expected from studies of the evolutionary status of such secondary dependants on human activity as pests and diseases. Examples of their response to selection are provided by the spread of races of citrus scale resistant to poisons, and the changes in the proportions of the physiological races of rust fungi which have been recorded over a period of years in the United States (Dobzhansky 1941). It is very evident in cotton, and probably applies equally to many other crops, that the development of the annual habit has been of first rate importance in making possible the cultivation of enormous populations of the host plant while minimizing by an annual close season the populations of its parasites.

An even closer relationship exists between the crop plants and man himself. Here, there is a true symbiosis, man being dependent for food upon his plants, and the plants benefiting by the clearing and weeding of the land, and the storing and sowing of the seed. It is not surprising, therefore, that there is a very close correspondence between the centres of origin and variability of crop plants and the centres of development of human civilization. Vavilov (1935) who has studied the centres of origin and variability of cultivated plants extensively, noted that these areas are in, or on the borders of, the areas of the major early civilizations. Four of his eight major centres cover the centres and environs of the ancient civilizations of Egypt, Mesopotamia, and the Indus. The other four occupy the areas of the early Peninsular Indian, Chinese, Peruvian, and Central American civilizations respectively. Examination of the history of the spread of cotton given in earlier pages indicates that this is no accidental circumstance, but results from the fact that the evolution of man and of his crop plants are mutually interdependent parts of the same process. The primary centre of origin of the Old World cottons in Sind falls in Vavilov's 'Middle Asiatic' centre, which includes Afghanistan and the neighbouring parts

of Asiatic Russia as well as India north and west of the Thar Desert. The main species centres, on the other hand, are in Vavilov's Indian and Chinese centres for *G. arboreum*, and 'Middle Asiatic' and 'Near Asiatic' centres for *G. herbaceum*. Considered as centres of diversification, without reference to the effects of cultural intercourse between human civilizations, the distribution among them of the variability of the Old World cottons appears to be of little significance. On the other hand, considered as areas in which human civilization grew as crop plants were domesticated and improved, they are of first importance for an understanding of the evolutionary process. The first development of cotton as a crop plant took place where the bread wheats, peas and other legumes, and a number of Cruciferous oil plants were added to the list of crop plants. With these new crops to fill its granaries, the Indus civilization flourished and spread. When it collapsed its barbarian successors fell heir to its crops, and spread them in their mountain valleys where great diversity is now to be found. Perennial cotton, being unsuited to cold winters, was confined to the plains, but having been distributed, along with its associated crop plants, into the Ganges valley through the Delhi gap, it was the textile plant of the people who discovered and domesticated rice. It is to the domestication of rice that the development of the civilizations of the coasts of the Bay of Bengal, and of Vavilov's Indian centre of origin of cultivated crops, can be ascribed. With a new basic cereal the food supplies necessary for civilization were assured, and the demand for accessory crops such as textile plants was increased. Thus to the rice civilizations must be credited the development of the *burmanicum* and *indicum* centres of variability in *G. arboreum*, from which race *sinense* developed in the east with the developing Chinese civilization, and race *bengalense* spread to the west to meet the newer demands of the ancient primary region. In like manner, the development of typical *G. herbaceum* in the valleys of the northward flowing rivers of Persia, Afghanistan, and Asiatic Russia resulted from successful selection in an introduced crop plant to meet the demands of civilized populations.

The growth in human population, and consequently in cultivated area and crop plant populations, following the acquisition of a food surplus by the domestication of a new cereal or the colonization of a new fertile region, would be followed by

TABLE II

Distribution of the centres of origin of cultivated forms of the world's most important crop genera (from Vavilov, 1935)

Genus	Centre of Origin							
	<i>Abyssinia</i>	<i>Mediterranean</i>	<i>Near Asia</i>	<i>Middle Asia</i>	<i>India</i>	<i>China</i>	<i>Central America</i>	<i>South America</i>
	VI	V	IV	III	II	I	VII	VIII
Starchy Grains								
<i>Hordeum</i>								
<i>Triticum</i>								
<i>Andropogon</i>								
<i>Avena</i>								
<i>Secale</i>								
<i>Eleusine</i>								
<i>Oryza</i>								
<i>Fagopyrum</i>								
<i>Panicum</i>								
<i>Zea</i>								
Legumes								
<i>Lathyrus</i>								
<i>Vicia</i>								
<i>Lens</i>								
<i>Pisum</i>								
<i>Cicer</i>								
<i>Dolichos</i>								
<i>Vigna</i>								
<i>Cajanus</i>								
<i>Glycine</i>								
<i>Phaseolus</i>								
Oilseeds								
<i>Guizotia</i>								
<i>Sinapis</i>								
<i>Linum</i>								
<i>Eruca</i>								
<i>Carthamus</i>								
<i>Sesamum</i>								
<i>Cocos</i>								
<i>Brassica</i>								
<i>Gossypium</i>								
<i>Arachis</i>								

Mean number of centres per genus : Starchy grains 2.1  
 Legumes 3.2  
 Oilseeds 2.9

an increase in crop variability. Differentiation by local adaptation would ensue, leading to the establishment of local races such as were detected in Indian crop plants by Hutchinson and Panse (1936). Personal preferences and special requirements lead to differentiation between the crops of neighbouring cultivators even in the same village (Hutchinson and Ghose, 1937a, Hutchinson *et al.* 1938). Yet apart from such minor distinctions, the variability in large tracts such as the Indian plains remains undifferentiated, and it is in the much subdivided populations of mountain valleys, where isolation and small population size have facilitated random differentiation, that crop plant variability is most striking. Hence in the diploid cottons, the variability of *G. herbaceum* in the valleys of Afghanistan is much more noticeable than that of *G. herbaceum* var. *acerifolium* in Western India, and in *G. arboreum*, the *cernuum-burmanicum* range in the mountain valleys of Burma and Assam appears very much greater than that to be found in race *indicum* on the plains of Peninsular India. For this reason, Vavilov's theory that the areas of greatest diversity are the centres of origin of crop plant species can only be accepted with the reservation that due allowance must be made for the effect of fragmentation of populations on the distribution of variability.

The intimate association between the rise of human civilization and the development of crop plants may be illustrated from the distribution of the centres of variability of the more important genera of crop plants. In Table II are summarized the distributions according to Vavilov (1935) of the centres of the ten most important genera in each of the three major groups of crop plants, starchy grains, legumes, and oil seeds. In order to keep the data strictly comparable, Vavilov has been quoted without alteration, although his views on the distribution of the variability in *Gossypium*, and possibly some other genera, require modification in the light of more recent data.

It is important to distinguish between the distribution of the centres of variability and the total area of distribution of the crop plant, but the close association between the centres of variability and the centres of origin of the crop, justifies their use as indicators of the original areas of domestication and primary dispersal.

Vavilov's centres may be grouped into three major regions, as follows:

A. Centres III—VI, corresponding to the 'Fertile Crescent' of Breasted (Childe 1942) in which the primary civilizations of the Nile, Mesopotamia, and the Indus developed.

B. India and China.

C. The New World.

Between these three great regions there was only a limited primary diffusion of crop plants. Only two of the ten genera yielding starchy grains have centres of variability in more than one major region. Oil seeds and legumes had a wider primary diffusion, four out of ten genera in each occurring in more than one major region. Within the major regions the distribution of starchy grains and oil seeds was more restricted than that of legumes. There was extensive primary diffusion between the centres included in the 'Fertile Crescent', as would be expected from the history of human intercourse in the area. In the region of the 'Fertile Crescent', it may be suggested that the great racial variability in mountainous tracts is chiefly the consequence of the isolation and random diversification there of crop plants originally domesticated in the neighbouring great river valleys.

No starchy grains have centres of variability in all three major regions, but one legume (*Phaseolus*) and one oil seed (*Gossypium*) have. *Gossypium* is among the less important oil seeds, and its wide distribution is no doubt to be ascribed to its importance as a textile raw material. Nevertheless the New World is poorly supplied with oil seeds, the only other one of importance being *Arachis*, and the possibility that cotton seed oil was used by early American civilizations is worthy of investigation. In legumes, also, the New World was deficient in genera, and *Phaseolus* beans were the main source of vegetable protein in pre-Columbian times. The similarity of the distributions of the crop plants of the two genera is highly suggestive, and a taxonomic, cytological, and genetic survey of the genus *Phaseolus* would form a most valuable parallel to that of *Gossypium*. Since no new character comparable with the lint of cotton is involved in the domestication of a plant producing an edible seed, there is no reason why species of the same genus of food plant should not be domesticated independently in the Old and New Worlds. Nevertheless, if the theory here advanced that cotton was taken across the Pacific as a cultivated plant is correct, it seems probable that other crop plants must have been carried over at the same time. Besides *Phaseolus* and *Gossypium*, only four crop plant

genera—*Solanum*, *Cucurbita*, *Amarantus* and *Canavalia*—are recorded as having centres in the Old and New Worlds. The distribution of the Old World centres of these six genera is given below:

Genus	Old World centres of origin			
	Near Asia IV	Middle Asia III	India II	China I
<i>Cucurbita</i>				
<i>Phaseolus</i>				
<i>Gossypium</i>				
<i>Solanum</i>				
<i>Amarantus</i>				
<i>Canavalia</i>				

Whether the New World representatives of other genera besides *Gossypium* were introduced there by civilized man, or were domesticated from New World wild species, can only be determined after extensive cyto-genetic studies, but one striking fact emerges. Five of the six genera have centres of variability in India, and of the three with centres in China, two have Indian centres also. The distribution of variability in the crop plant genera common to both Hemispheres, therefore, supports the theory of a trans-Pacific rather than an Arctic link between them. Vavilov (1935) separates Indo-Malaya as a minor centre subsidiary to the Indian centre. The Indian centre is characterized by a very heavy preponderance of plants reproduced by seed, whereas the bulk of the Indo-Malayan plants are vegetatively propagated. Since none of the Indo-Malayan plants—not even the coconut—have been established in the New World long enough to have developed centres of variability, it is evident that the trans-Pacific migration was carried out by people with direct contact with India, and not by a race long established in Indo-Malaya. In particular, the migrants cannot have been of the Polynesian stock, since the Polynesians are expert in the care of vegetative propagating material during long sea voyages, and have also distributed the coconut far and wide in the Pacific region.

All the available evidence supports the view here put forward

that the domestication and distribution of crop plants, and the development and conservation of variability within them, are intimately bound up with the origin and spread of civilization, and that the whole interrelated complex, including civilized man, his domestic animals and his crop plants, has grown from a single root and spread to the New World by trans-Pacific migration.

## V. CONCLUSION

THE wisdom of planning crop research to cover the whole of the crop plant genus has been abundantly proven. When the Cotton Research Station was started, the practical value of the wild species was limited to the rather doubtful possibility of transferring genes for disease resistance from them to the cultivated cottons. Nevertheless, studies of their taxonomy, ecology, distribution, cytology and crossing behaviour were undertaken as essential to a proper understanding of the genetics of the cottons. In the event, the belief that knowledge of the wild species would be essential for an evaluation of the status of the cottons was fully justified. Moreover, when the development of methods of inducing polyploidy opened up possibilities of synthesizing new allopolyploid cottons, the information available from studies of wild species was invaluable in assessing the possibilities of making new and useful genom combinations.

The study of variation and differentiation in the genus as a whole, is fundamental to the rational exploitation of variability in the acclimatization of cottons in new areas, and the development of lint characters to meet the demands of the cotton industry. The spread of Upland cotton, first in the Southern States of the United States, and thence into India, Russia, Africa, and other cotton-growing countries of the Old World, has led to over-emphasis on the value of the varieties of the American Cotton Belt. The demonstration that other Upland stocks are available will result in a wider choice of material from existing sources, and the genetic analysis of the behaviour of inter-varietal hybrids in *G. hirsutum* will encourage the synthesis of new variable material by hybridization.

The outstanding feature of the discussion of differentiation in *Gossypium* has been the importance of variability, and despite the need for uniformity in the product to meet market requirements, future breeding programmes must be designed for the maintenance of variability instead of for the isolation of pure lines. The background of knowledge necessary for the develop-



ment of such new breeding methods will come from the field of population genetics and crop variability studies, and its successful application will depend upon the fusion of genetics and plant breeding into a single science.

The trend towards the integration of specialist sciences goes further than the development of applied genetics. The interrelations of genetics and ecology have been demonstrated by Hutchinson and Ghose (1937a), the importance of developmental studies in the interpretation of genetic data by Stephens (1944f), and the significance of physiological factors in breeding for yield by Manning (1945). The crop biology of the future will be a single science, and its success will be in proportion to the degree in which specialist studies are made to serve the needs of co-ordinated research.



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